

THE SARRACENIA RUBRA COMPLEX

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INTRODUCTION AND HISTORY

In his "*Flora Carolina*", 1788, Walter described *Sarracenia rubra*. MacFarlane, in his monograph of the "*Sarraceniaceae*" (1908), treated *S. rubra* in a broad sense and did not name any forms or varieties.

In 1929, E. T. Wherry described *Sarracenia jonesii* from Flat Rock, North Carolina, as a separate species closely related to *S. rubra* Walt. According to Wherry, the range of *S. jonesii* extended from the mountains of Henderson and Buncombe Counties, North Carolina, southwestward through Alabama to the coast of western Florida and into eastern Mississippi.

In 1949, C. R. Bell published his "A Cytotaxonomic Study of the *Sarraceniaceae* of North America." In this work, he reduced *Sarracenia jonesii* to the rank of forma under *S. rubra* Walt., including in forma *jonesii* all herbarium specimens from the known range of the entire *S. rubra* complex that showed leaves with sharply expanded upper pitcher tubes.

S. T. McDaniel, in his doctoral thesis (1966), further reduced *Sarracenia jonesii*, considering that it had no taxonomic status.

From the time of Bell's work, botanists and carnivorous plant buffs interested in *Sarracenia* have argued pro and con considering the validity of *S. jonesii* and the nature of *S. rubra*. Almost every discussion appearing in print presents a different view. After much discussion by others, Wherry, in 1972, reduced *S. jonesii* to the rank of subspecies under *S. rubra*, and recognized that its range was limited to the mountains of North and South Carolina.

Our interest in *Sarracenia rubra* began about 1953 when our own field studies, experiences, and observations seemed at odds with published information. Our observations and

studies over more than 20 years have led to the description of a new species, *S. alabamensis* Case & Case (1974), and to the conclusion that "*S. rubra*" represents a complex of taxa, all related, yet in some ways all subtly distinct. Before we present our data, we believe it will be helpful to consider the important taxonomic characters used by botanists in delineating species of *Sarracenia* and some of the problems involved.

SIGNIFICANT TAXONOMIC CHARACTERISTICS

The structural features most significant in distinguishing species of *Sarracenia* include leaf shape and size, types of leaves produced, size, shape, carriage and reflexion of the pitcher hood, presence or absence on the leaf of window-like areoles, details of leaf coloration, pubescence and substance.

Wherry apparently considered leaf size of prime importance in his early study of *Sarracenia jonesii*, but Bell (1949), commented as follows:

"Size is of no value per se in species delimitation in this genus. Various ecological factors result in mature plants of many sizes within a given species. The extreme cases of this are shown in *S. minor* and *S. flava*, but less striking differences in size appear in all other species of *Sarracenia*. Size, therefore, is not a constant, and cannot be used as a basis for taxonomic differentiation."

We agree with Bell that ecological factors can produce great size variation among wild individuals of any species grown under diverse conditions; indeed, we feel that this ecologically induced variation is responsible for much of the past confusion in the *S. rubra* complex. We further agree that an occasional aberrant variant can occur within any given species, but we cannot agree that size in general terms is not constant; rather all of our studies indicate that there *are* definite, genetically controlled size trends for leaves and leaf parts in all species of *Sarracenia*. It is

not that size is of no value, but that ecological factors, acting upon developing leaves, affect the expression of leaf size and shape.

Within the parameters we have discussed in this paper, we agree completely with Bell (1949) when he says; "The over-all shape or form of the pitched leaves is generally a constant morphological characteristic, and as such is the most useful single feature used by taxonomists in species delimitation within the genus *Sarracenia*."

While flower structure is most distinctive at the genus level, only petal color, petal shape, and to a lesser degree, flower size and scent have been used in species demarcation. Flower size is related not only to the species involved, but is also affected by the ecological situation, age, and vigor of the plant. The later flowers on a given plant tend to be reduced in size, sometimes significantly so over the earlier ones. There is enough overlap of size, petal shape, and scent between various species to render flowers of limited value for taxonomic differentiation.

The taxonomic usefulness of the leaf over the blossom in *Sarracenia* must be considered in light of the specialized function of the leaf. The hollow, tubular leaf is a pitfall, passive trap, complete with baiting fluids which paralyze or poison insects, as shown by recent studies (Sci. News 106: 286. Nov. 2, 1974).

Plummer, *et al.* (1964) found that nutrition through insect trapping affects pitcher plant growth rates far more than had previously been appreciated. We found that we could bring two-inch plantlets of *Sarracenia flava*, *S. jonesii*, *S. alabamensis* subsp. *wherryi* \times *S. minor*, and others to near flowering size in as few as 9 or 10 artificial feedings through the pitchers, about a month apart, while control seedlings scarcely grew at all.

In investigations related to his doctoral dissertation now in preparation, Thomas Gibson (personal communications, 1974-1975) has clearly established that when several species of sympatric sarracenias grow in the same bog, they

trap different species of native insects with little overlap between species.

It seems to us that there is sound evidence in *Sarracenia* of growth, competition, and survival factors which involve the trap-leaves. It is not surprising, then, that it is the leaves which have undergone the striking evolutionary changes and that floral structures have evolved less and are of less value in taxonomic studies. The principal works of the past, e.g., MacFarlane (1908), Harper (1918), Wherry (1929, 1935), Bell (1949), and McDaniel (1966, 1971), have made use of this leaf diversity; their works and identification keys make use of leaf structures coupled with petal color almost exclusively.

We have concluded that pitcher size of the largest leaves of the growing season, orifice width, hood length and width, scape height, and an index derived by dividing hood length by width yield the most reliable measurable data for pitcher comparison. When these data are related to color of mature, hardened leaves, venation patterns, hood carriage and reflexion, ratio between scape and leaf height, leaf substance and pubescence, overall flower size, petal shape, size and color, and geographic distribution, definite patterns emerge.

ECOLOGICAL RESPONSES DURING LEAF DEVELOPMENT

In a genus in which leaf characteristics assume great importance, it is essential to realize how ecological conditions affect leaf development. This is particularly so in *Sarracenia* where the unique, hollow pitcher complicates ecological response. Many factors directly affect leaf development; our observations and the meager published observations indicate that the response of leaves is essentially the same in all species.

MacFarlane (1908) comments that coolness, shade, and moisture all cooperate to affect reduced pitcher cavity, color intensity, and conformation of the laminar wing in all species, but he cites no definite experimentation. Bell

(1949), in considering *Sarracenia psittacina* discusses the influence of light upon its leaves:

The leaves however, do show the effect of strong sunlight. Leaves of plants growing in shaded locations tend to be longer, greener, and have smaller hoods than those grown in the sun, which are often found with large hoods and almost solid red leaves.

Bell (1949, pp. 157, 158) also discusses the fact that red color of both leaf and flower in *Sarracenia purpurea* is influenced by intensity of sunlight. Wherry (1933), in discussing *S. purpurea* var. *heterophylla*, discusses the nature of the type specimen of *heterophylla*, and ascribes its elongated leaves to shading. Mandossian (1966) reports a laboratory experiment designed to test the effect of light intensity upon production of pitcher volume and lamina development in Michigan *S. purpurea*. She concluded that low light levels result in large, highly developed pitcher lamina and in "absorption" (reduction) of the pitcher. That this is true under both laboratory and field conditions, we can verify.

Unfortunately we have seen no thorough discussions of changes in leaf shape correlated with light intensity in the trumpet-leaved pitcher plants. But we have grown all species for over 20 years in our comparative cultures and out of doors, and have observed them in the field. All of the trumpet-leaved species respond in a similar manner. Given other requirements, growth is most vigorous and coloration most intensely developed in full sunlight. The pitchers, with relatively short, strong petioles, stand properly erect, with fully expanded pitcher and hood.

If light decreases from that of full sunlight intensity, changes occur in developing leaves. New leaves elongate significantly over previously formed leaves; petioles become weak; pitcher volume may at first increase slightly, but if shading persists, subsequent leaves become reduced in size and pitcher volume. The wing or lamina of the pitcher enlarges, especially in the mid-region of the pitcher.

The increased laminar wing warps the pitched section into abnormal positions. In most species, the pitcher hood at first enlarges, but is ultimately sharply reduced. In heavily shaded specimens developing hoods may have difficulty in assuming a normal carriage.

In most species flowering is heaviest in fully sunlit plants. As light is reduced, flowering decreases. Heavily shaded plants seldom bloom at all, although members of the *Sarracenia rubra* complex, somewhat better adapted to brushy, shaded habitats than most species, retain the ability to flower sparingly even when shade-induced leaf deformation is considerable.

All sarracenias are hydrophytes. Other conditions being equal, the maximum growth potential of leaves is reached in the presence of an abundant water supply. If the water supply is reduced to a minimum that will maintain life for the pitcher plant at a time when it produces new leaves, changes in leaf form result, which are similar in all species. Pitcher volume becomes reduced, and the laminar wing increases markedly in proportion. In trumpet-leaf types such as *Sarracenia rubra*, new leaves become shorter, less inflated, often with hoods that barely open. Less anthocyanin pigment develops. In taxa which normally produce more than one set of pitched leaves in one season, excessive dryness may result in failure to produce late season pitchers, or in the production of stunted ones.

The amount of peaty, organic material in the soil influences pitcher size in all *Sarracenia*, provided other requirements are met. Harper (1918) and Bell (1949) report unusually large leaves on *S. minor* growing on floating islands of rotting vegetation in Okefenokee Swamp, Georgia. Bell reports that leaves of these large forms reverted to a smaller, more typical form under his greenhouse conditions. Presumably the highly organic substrate plus abundant water influenced leaf size in the wild plants.

On the inner Coastal Plain near Lucknow, South Carolina, and in the Fall Line Sand Hills of Taylor County, Georgia, we collected large-leaved plants of *Sarracenia*

rubra. Shaded specimens, especially from the Georgia station, were very tall, reminiscent of *S. jonesii* Wherry. When removed to our greenhouses and grown in our prepared, uniform soil mix, all plants from these areas gradually reverted to a size typical of *S. rubra* from the more sandy, outer Coastal Plain soils.

Mandossian (1966), working with *Sarracenia purpurea* in Michigan, found that pitcher plants growing in a marly, mineral-type soil formed many crowns and numerous small pitchers; those in highly organic sphagnum bogs made fewer crowns and leaves, but were larger, more fully expanded. Reciprocal transplants readjusted morphologically in a very gradual manner; she found that plants needed at least two growing seasons to adjust leaf size and form from that typical of one habitat to that typical of another. She further cites the work of others to show that gradual adjustment of form over a long period is characteristic of many other plant species.

Ecological factors appear to influence pitcher plant leaf development strongly. One must use caution, therefore, in comparing similar leaved taxa unless they have developed under identical conditions for a considerable period of time.

SCOPE OF THE PRESENT STUDY

Our study of the *Sarracenia rubra* complex has been four-fold: 1) extensive field observations, 2) nearly 20 years of comparison of live material from all known "*S. rubra*" populations grown under standardized conditions in our greenhouses, 3) comparison since 1970 of plants of all populations grown out of doors in an artificially created wet sand bog, and 4) extensive leaf analysis utilizing not only material from our culture experiments, but also of specimens deposited in the herbarium collections historically important to this problem.

We performed minimal chromosomal studies, as the work of Bell (1949) and Hecht (1949) indicates that $n = 13$, $2n = 26$ in all species. The small size and size range of

the chromosomes in the entire genus (Bell, 1949) and in the "*S. rubra*" taxa in particular, and the difficulty of obtaining really good root tip observations in this genus, make karyological studies difficult. There is need for additional work. For chromatographic examination of the complex, we consulted specialists; their findings are generalized in this paper, and will be separately published by them.

FIELD POPULATION EXAMINED

We examined the major population centers of all species of *Sarracenia* so that we might understand the influence of hybridization and introgression upon the group. For all species which enjoy an extensive range, we visited a number of stations at various distant points within that range so as to obtain a broad sampling of study material. We have observed them at all seasons, winter, flowering, young leaf development, mature leaf, fruiting; in all we have examined thousands of living plants in the wild.

If one consults the distribution maps for *Sarracenia rubra* (sensu Bell, 1949, plate 12) or as treated by McDaniel (1966), one obtains the impression that "*S. rubra*" grows in suitable habitats more or less uniformly across the area of its range as shown on the maps. Our field studies do not confirm this. We found that there appeared to be five disjunct populations; four of these showed what we consider to be distinctive structural and behavioral differences.

If one plots the localities for existing herbarium specimens on a map, the distributions also fall into five disjunct groups which approximate the ranges of the populations as we determined them from our field studies of the past 20 years (see Fig. 1).

For our field observations and our comparative culture studies of the *Sarracenia rubra* complex we observed populations and obtained cultures from the following states and counties: Alabama: Autauga, Baldwin, Chilton, Elmore, Escambia, Mobile, Washington. Florida: Okaloosa, Santa

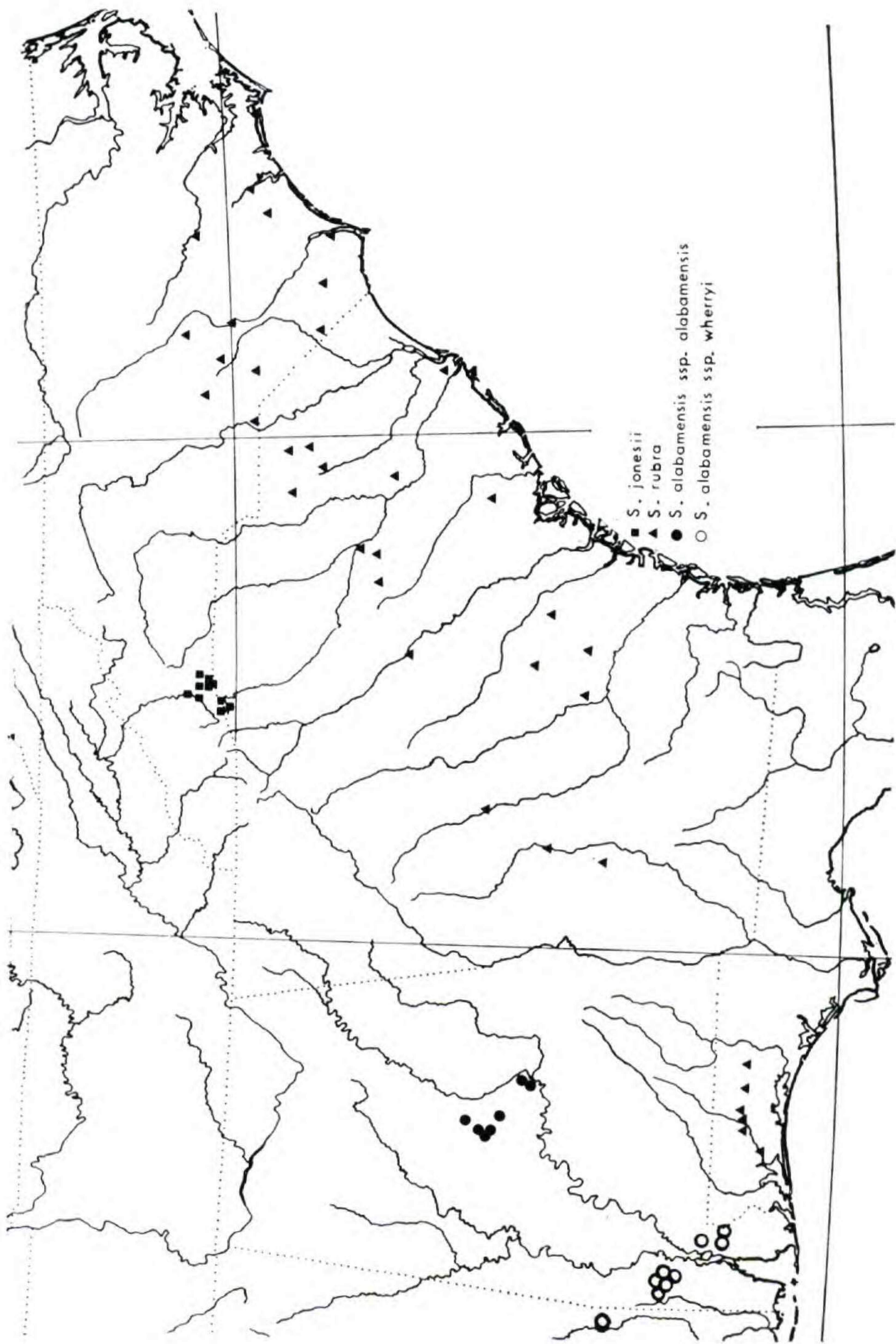


Fig. 1. Distribution of the *Sarracenia rubra* complex as determined by existing herbarium specimens which we have examined.

Rosa. Georgia: Taylor. North Carolina: Bladen, Brunswick, Columbus, Henderson, Transylvania, Buncombe. South Carolina: Georgetown, Horry, Kershaw, Lee, Pickens. Mississippi: Wayne.

Most of our observations on the various populations, based upon both field work and comparative culture, are summarized in Table 2, or in the taxonomic treatments in this paper.

MEASUREMENT PROBLEMS

In 1956, and again in 1972-75, we examined all the specimens of the *Sarracenia rubra* complex from the following herbaria: US, PH, PENN, NCU, NY, FSU, (1972-75 only) and Duke (1956 only).¹

Many herbarium specimens are very difficult to compare with others. They are collected at nearly all seasons of the year; many are taken in flower and either lack leaves of the current season, or are taken with leaves not yet fully expanded. Pressing of the tubular leaf distorts the carriage and reflexion of the pitcher hood. Drying often destroys external pubescence, distorts substance, and destroys the subtleties of leaf color.

In addition, there was often the haunting suspicion that with the larger-leaved taxa, many herbarium specimens had been taken to fit the herbarium sheet rather than to represent the typical plant.

Our field observations, the published remarks of others, and the diversity of the herbarium specimens made us question whether the herbarium comparisons would be reliable. This concern proved to be unfounded (see fig. 2).

Another problem arose at this time. Past authors gave leaf measurements in broad general size ranges only. Since members of the *Sarracenia rubra* complex can produce

¹We wish to thank the curators of the herbaria whose specimens we have studied. We are grateful to Dr. W. H. Wagner, Jr., University of Michigan, and to Dr. James Wells, Cranbrook Institute of Science, for their valuable counsel and for securing the specimen loans for us at various times in this study.

pitchers of many sizes on a given plant, a need to standardize comparisons and measurements seemed to us essential. We determined, therefore, to define our own leaf and hood measurements, thus hoping to eliminate the changes in hood carriage (and hence height) caused by pressing of specimens. We also determined to devise a standardized method of comparative culture which would eliminate as many of the ecological variables as possible.

MEASUREMENTS

MacFarlane (1908) pointed out that seedling leaves in all species of *Sarracenia* tend to resemble closely those of *S. minor* Walt., and do not show well the specific differences. We might not agree that all seedling or juvenile pitcher-leaves resemble *S. minor*, but our observations do show that specific differences show most clearly in the largest leaves of a growing season of vigorous flowering-size plants growing in full light. In order to standardize comparison of the taxa in our comparative cultures, we measured only the two largest leaves produced by a flowering rhizome terminus of a given clone that season. For herbarium material, the only standardization possible was to measure the one or two (if present) largest complete leaves on the specimen.

MEASUREMENT TECHNIQUE

We measured pitcher leaf length from the point of attachment of the amplexicaul base to the rim of the pitcher orifice. Such leaf measurements do not include the hood. Hood length refers here to the distance from the narrowest part of the hood constriction (or neck) to the tip of the hood, while hood width refers to the distance across it at its widest point.

To facilitate measurement comparisons of the tubular pitcher between fresh and herbarium materials, we give width figures for flattened pitchers rather than diameters for expanded ones.

Scape height measurements run from point of basal attachment to the attachment of the sepals. Petal length and width represent the structure's greatest dimensions.

There are distinctive differences in pitcher taper and expansion in the *Sarracenia rubra* complex. These are subtle, and can be affected by ecological factors present as the leaf develops. The same is true for the carriage of the hood over the pitcher orifice and its manner of reflexion. Color patterns vary not only among the populations, but in the same taxon or clone in relation to leaf age, health, and the amount of sunlight the leaf received. We found no truly satisfactory method to measure these characteristics statistically. Yet there are characteristics distinctive to each population. These are best described or illustrated in the appropriate sections of this paper.

COMPARATIVE CULTURE METHODS

We brought together, in our greenhouses at Saginaw, Michigan, plants of each of the taxa collected by us from the wild. We chose plants at random, where possible, but we did make an effort not to select plants of obviously hybrid origin. We grew our plants in an east-west oriented Everlite greenhouse. We placed the plants to be compared on the benches in north-south rows so that all plants would receive approximately equal lighting during the day and none would seriously shade the others. Tops of the plastic flowerpots stood above the base of the greenhouse glass; thus the plants received maximum available light. No shading was used on the glass of the greenhouse, and plants received full sunlight throughout the day, excepting in very late summer, when the plants were shaded from direct sun's rays after 3:00 P.M. by a nearby building, but there was always open sky directly overhead. Light was uniform and strong; during July and August, 1974, we checked the intensity of the light daily between 11:00 A.M. and 2:00 P.M. with a Gossen, Luna-Pro incident light

meter. We found the plants received 4,000 to 8,000 foot-candles of light, depending upon the degree of cloudiness.

Plants received the normal photoperiod for this latitude. In winter, we gave them a dormant period at $\pm 0^{\circ}\text{C}$ for two months. Growth commenced in late February, and the plants in the greenhouse here bloomed at the same time as that usual for wild plants in the Gulf Coastal states, i.e., early April.

During the summer months, open windows and doors admitted many insects which the pitcher plants captured in great numbers.

To provide a uniform growing medium to all plants, we compounded soil using six parts washed silica sand (obtainable at builder's supply stores) with four parts commercially packaged Canadian (sphagnum) peat, thoroughly mixed together. Rhizomes were planted at the surface of the mix.

To assure uniform moisture to all plants, we made trays approximately two inches deep and lined these with 10 mil polyethylene sheeting to make a shallow tank. Pots stood in this tank with the soil surface approximately 5 inches above the water level; all pots received the same water supply. The water used came from a surface well which drained from acid sands; its pH averages 6-6.5, and the native vegetation in the damp places near the water source included such acid-soil and bog plants as *Vaccinium* sp., *Sphagnum* sp., *Osmunda regalis*, *Liparis* sp., and *Spiranthes* sp.

Specimens used in our comparative studies grew under these conditions for at least three years, most of them for more than 10 years.

In all cases, their growth was in every way typical for all known species of *Sarracenia*, and our plants produced vegetative parts which were within the size ranges of the existing herbarium material from the same areas as our study plants and within the size ranges of plants we have observed in the field.

FINDINGS

Figure 2 shows leaf size ranges from 6 distinct population areas representing 4 taxa. Figures 3 and 4 present data on pitcher size vs. hood length/width ratios for the 6 populations. Analysis of measurable data for several useful taxonomic characters is compiled in Table 1.

To determine if the population differences represented chance variation or whether the variation was significant, we performed an analysis of variance on the five leaf and scape measurements (see Table 1), and found in each case that the degree of significance was well above the 0.5% level, indicating that the chance that these specimens belonged to a single population was extremely small. The specimens of the Taylor Co., Georgia, area and those of the disjunct western Florida area, while differing from the plants of the Carolina-Georgia Coastal Plain area in leaf size and shape, differed from them to a much lesser degree than those plants differed from other populations. When this information is coupled with other structural similarities shared by these populations and not found in the others, and with what we believe has been the geological history of the group, we considered that these particular populations, even though disjunct, represent one specific entity.

In all measurements, our data on the 6 populations show significant grouping into 4 structurally distinct taxa, both for comparative culture and for wild specimens. We had not expected that the wild specimens would show the natural groupings so clearly, in view of the great influence ecological conditions exert over pitcher size and conformation in *Sarracenia*. The smaller sizes of the comparative culture material over wild (fig. 2) reflect the response of the material to uniform conditions in which shade effects (etiolation), moisture, and soil differences were eliminated. Our comparative culture material we consider to represent healthy, normal plants; many of our study clones have thrived in our culture for 10-20 years, all bloom profusely,

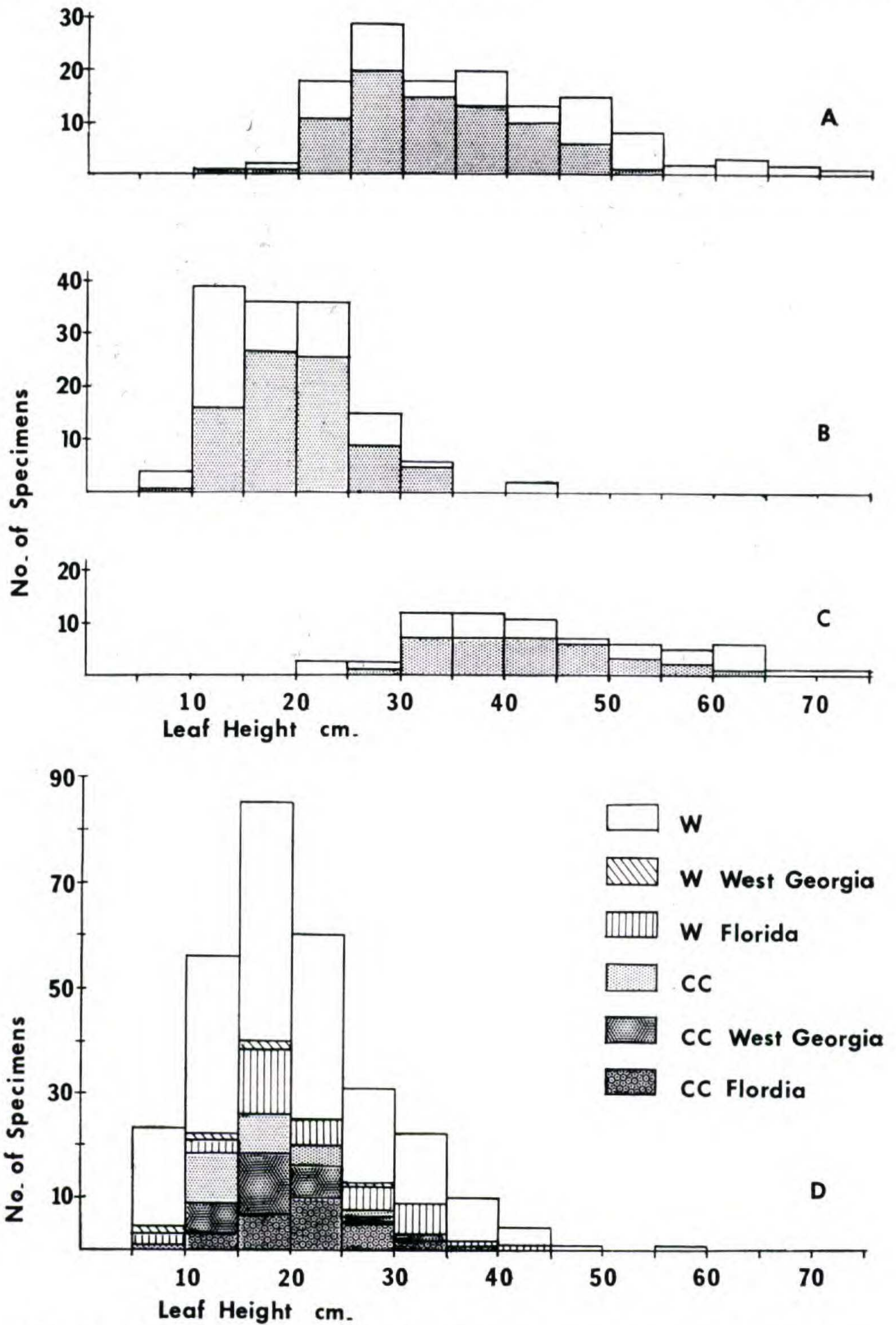


Fig. 2. Leaf height and number of specimens examined for 4 taxa comprising the *Sarracenia rubra* complex. W = wild (herbarium specimens), CC = our comparative culture material. The taxa are: A, *S. alabamensis* subsp. *alabamensis*; B, *S. alabamensis* subsp. *wherryi*; C, *S. jonesii*; D, *S. rubra*.

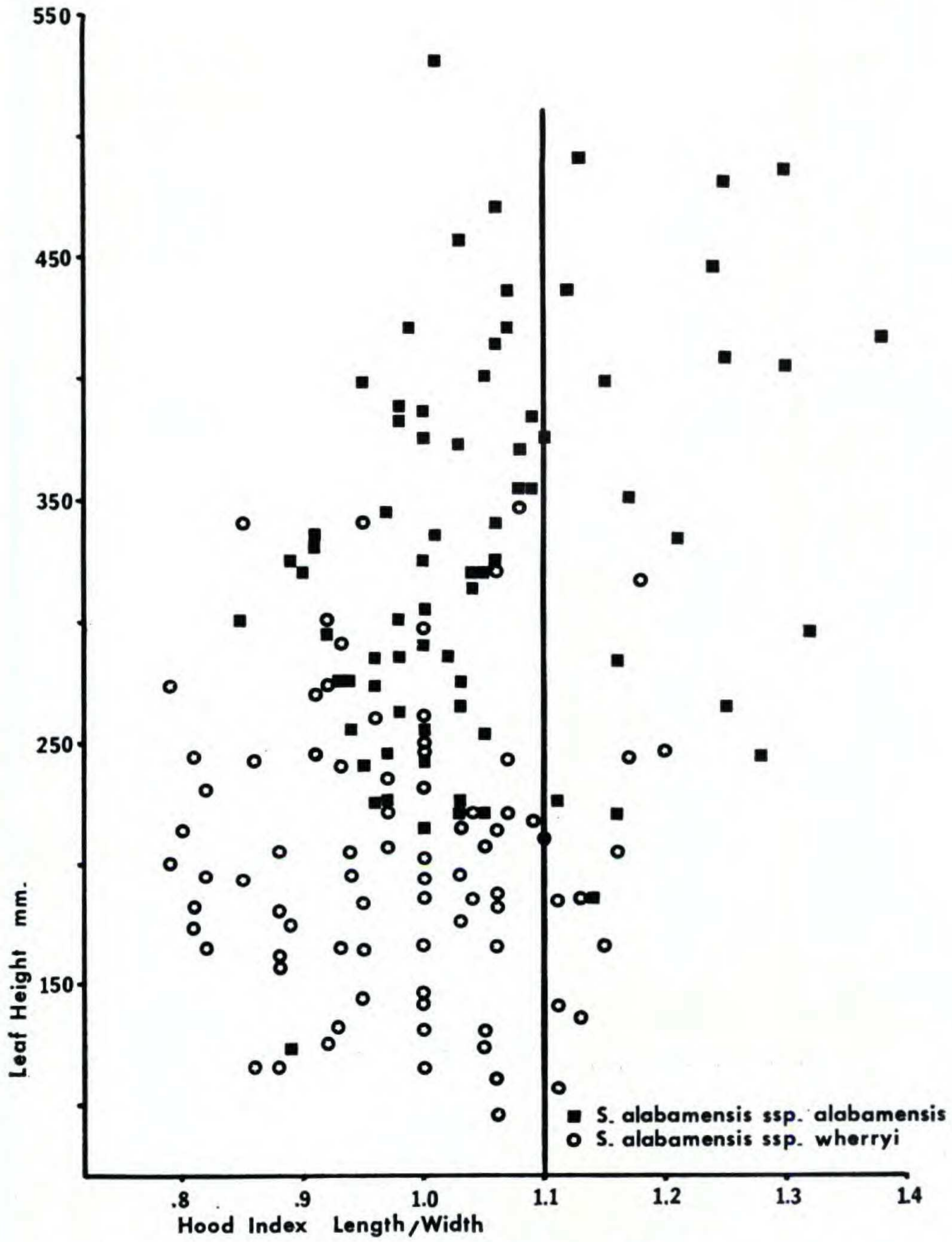


Fig. 3. Leaf height and hood length/width index comparison for *Sarracenia alabamensis* subsp. *alabamensis* and *S. alabamensis* subsp. *wherryi*.

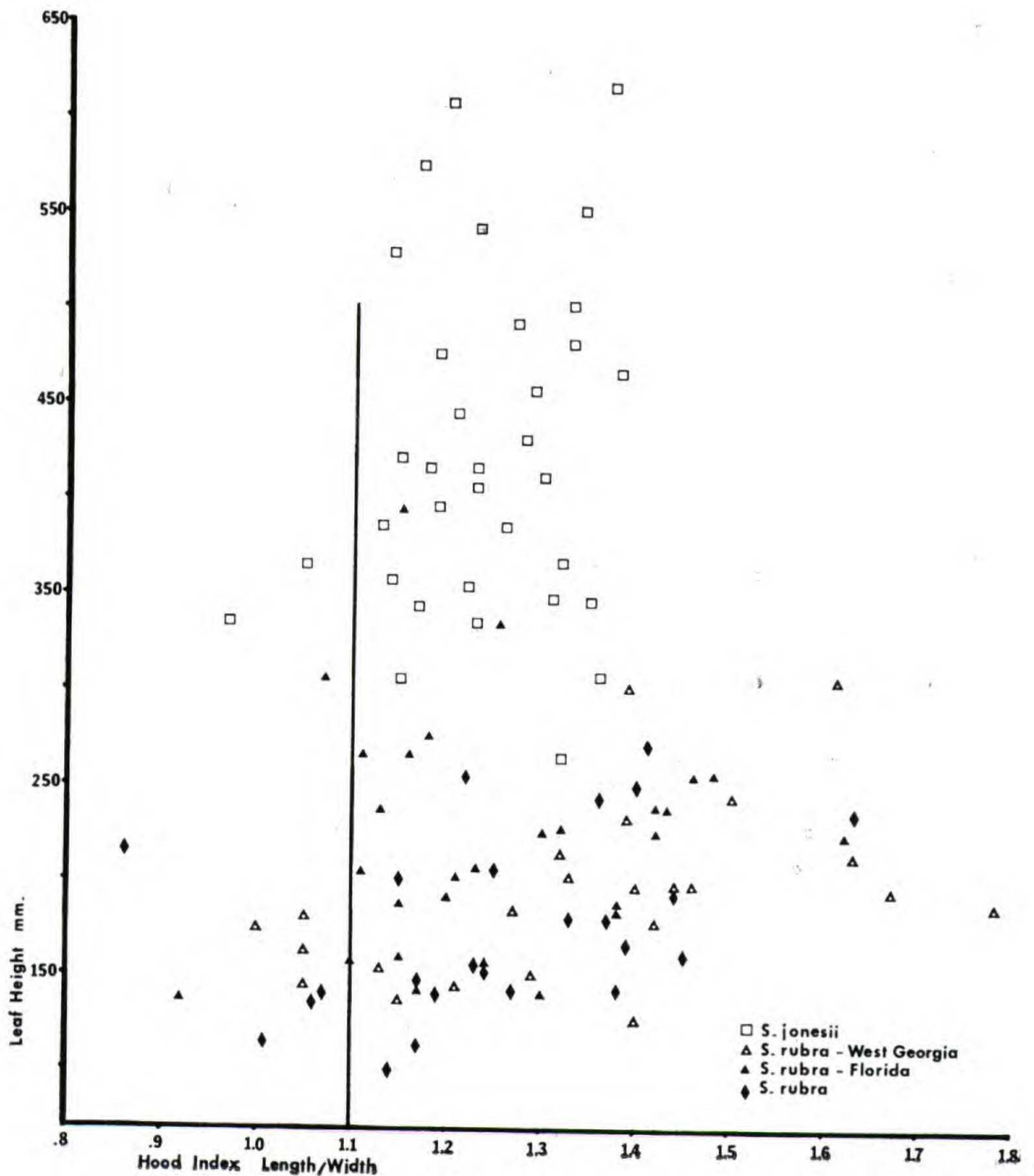


Fig. 4. Leaf height and hood length/width index comparison for *Sarracenia jonesii* and *S. rubra*. The *S. rubra* from 3 extremities of its range are plotted separately: diamond symbol = *S. rubra* of the Carolinas, both inner and outer Coastal Plain stations, open triangles = *S. rubra* from the inner Coastal Plain, Fall Line hills of Taylor Co., Ga., (a possible disjunct colony), and solid triangles = *S. rubra* from the disjunct, Western Florida population.

Table 1. Analysis of measurable data on the two largest leaves available for leaf height, leaf structures, and scape height for both our comparative culture specimens and herbarium specimens (in mm). W = wild or herbarium specimens, CC = comparative culture material. M = mean, s = standard deviation, r = range, and n = number in the sample. F*, in the F distribution, a number larger than 2.7 would indicate a significance beyond the 5% level; a number greater than 4.5 would indicate a significance beyond the .5% (F .995) level.

	Leaf Height		Orifice Width		Hood Length		Hood Width		Hood Index (Length/Width)		Scape Height		
	W	CC	W	CC	W	CC	W	CC	W	CC	W	CC	
<i>S. alabamensis</i> <i>ssp. alabamensis</i>	M	408.6	330.5	26.9	35.8	39.7	50.8	33.4	48.5	1.18	1.05	398.0	443.2
	s	140.5	82.7	10.2	8.2	14.9	12.1	11.0	11.2	0.17	0.11	83.5	62.8
	r	185-717	122-530	7-48	17-67	7-71	25-90	8-50	22-88	0.81-1.58	0.85-1.38	270-571	320-572
	n	52	78	51	78	40	76	40	76	40	76	35	14
<i>S. alabamensis</i> <i>ssp. wherryi</i>	M	183.2	201.7	14.6	19.8	22.0	27.2	21.1	28.0	1.05	0.98	264.0	302.3
	s	79.3	56.7	4.6	6.1	9.3	7.8	8.2	8.6	0.16	0.10	73.4	59.0
	r	80-450	95-347	7-28	9-42	8-45	17-46	8-40	13-54	0.67-1.7	0.79-1.2	137-385	227-455
	n	55	84	54	86	44	85	44	85	44	85	35	14
<i>S. jonesii</i>	M	445.3	422.8	28.4	23.1	45.2	42.3	36.7	34.4	1.24	1.23	442.6	498.7
	s	142.7	87.1	8.0	5.2	10.5	7.8	7.4	6.5	0.21	0.12	111.0	104.2
	r	210-730	262-615	10-42	15-42	24-65	26-57	24-54	20-50	0.91-1.67	0.97-1.38	325-690	351-696
	n	33	34	30	34	20	34	20	34	20	34	23	28
<i>S. rubra</i>	M	208.3	196.4	12.0	15.1	23.3	26.4	16.2	20.6	1.46	1.29	379.7	459.2
	s	89.1	54.3	4.8	5.7	7.1	8.3	5.9	6.1	0.41	0.19	90.7	109.2
	r	57-570	100-395	5-28	7-40	7-45	14-53	7-39	9-38	0.8-4.3	0.86-1.78	170-630	293-661
	n	216	79	189	79	90	78	90	78	90	78	117	44
F	99.1*	131.8*	116.4*	141.5*	48.3*	120.4*	63.3*	144.1*	19.9*	80.4*	22.3*	14.7*	

TABLE 2

Characteristic	<i>S. jonesii</i>	<i>S. rubra</i>	<i>S. alabamensis</i> subsp. <i>alabamensis</i>	<i>S. alabamensis</i> subsp. <i>wherryi</i>
Pitcher types	all alike	all alike	spring pitchers small, all alike sigmoidly recurved wing broad, volume small, green-bronze. Summer and fall pitchers large and voluminous, bright yellow-green.	
LARGEST LEAVES:				
Height & width	tall and thin	short and thin	tall and wide	short and wide
Petiole	long; $\frac{1}{4}$ to $\frac{1}{3}$ length of pitcher	very short; less than $\frac{1}{4}$ length of pitcher	medium; about $\frac{1}{4}$ length of pitcher	short; less than $\frac{1}{4}$ length of pitcher
Pitcher chamber	expanding rapidly in upper $\frac{1}{4}$. Somewhat bulged on abaxial surface below hood neck	very gradually tapered from base to orifice	expands uniformly but rapidly widening to wide orifice	expands from leaf base gradually to orifice, often widest just below orifice
Upper pitcher tissue substance	firm, thick, waxy; glabrous to puberulent	very firm, thick, waxy; glabrous to puberulent	thin, soft; densely fine pubescent	soft; very densely fine-pubescent

Orifice rim	scarcely or not flared, rim tightly rolled, narrow	not flared, tightly rolled, narrow	strongly flared, loosely or irregularly rolled	weakly flared or not flared, moderately tightly rolled
Rim color	green to dark maroon	dark green to maroon	iridescent-light yellow-green	yellow-green, rarely maroon flushed (hybrids?)
Rim carriage	horizontal or gradually sloping downward from hood to wing	horizontal or barely deflexed at orifice wing juncture. Most often raised slightly at juncture	tapering gradually downward to wing juncture, but with a large spout-like indentation at juncture	variable, but with a noticeable downward indentation at region of orifice wing juncture
Markings: Color of mature sunlit leaves	green, upper leaf veins and sometimes other tissue suffused with dark maroon-purple, particularly on inside of hood neck	dull green, young leaves suffused with reddish-brown which is replaced in most mature leaves by a dark maroon overlay; veins dark maroon	yellow-green over-flushed faint red until mature, becoming light green or golden-green in upper portion	dull light green, bronze-red flushed
	veins colored on both outer and inner surface of pitcher	veins colored on outside and inside of pitcher	veins colored maroon on inside pitcher surface only	veins mostly colored on inner pitcher surface, color may show through to outside
			faint whitish-green areoles irregularly present	

TABLE 2 — Continued

Characteristic	<i>S. jonesii</i>	<i>S. rubra</i>	<i>S. alabamensis</i> subsp. <i>alabamensis</i>	<i>S. alabamensis</i> subsp. <i>wherryi</i>
Hoods	longer than wide; generally longer than wide; cordate, green or maroon flushed, veins colored on both surfaces to hood margin; slightly reflexed	generally longer than wide; ovate, veins of both surfaces colored to margins; not reflexed; veins of neck very strongly colored forming a distinct dark patch	often wider than long; upper surface convex-puckered; clear golden-green, outer veins green or faintly colored in proximal ½ only; strongly reflexed	usually as wide or wider than long; green-bronze flushed; main veins of inner surface colored maroon, outer surface often all green, rarely colored; slightly to moderately reflexed
Phyllodia	faintly undulate	not undulate	broadly undulate	convex, weakly undulate to not undulate
	none	none	very occasional, flat and recurved; produced in early summer	none
Rhizome branching pattern	moderate, small clumps unless disturbed	moderate, forms small clumps	strongly branching, forms large, dense clumps	sparse to small clump former
Relative bloom time in comparative culture	late, last to bloom 7-9 days after <i>S. rubra</i>	late-mid season, starts as <i>S. alabamensis</i> finishes	starts 10 days after subsp. <i>wherryi</i> , early mid-season	very early, first to bloom

Petal carriage	flat, pendant, not spreading	flat, pendant, lateral spreading- pendant, margins of distal lobe flat frequently inrolled	flat, pendant, distal lobe becoming reflexed (from <i>S. alata?</i>)
Sepal carriage	moderately reflexed	very strongly reflexed	strongly reflexed
Winter photoperiod response (not frozen)	nearly evergreen	essentially evergreen	partially dieback, leaf bases evergreen
			weakly reflexed to flat and falcate-curved
			nearly total dieback

Table 2. Comparison of the 4 taxa of the *Sarracenia rubra* complex for some useful distinguishing features not easily measured.

and the size ranges of our specimens are within the size ranges of wild specimens from the same localities. Our largest leaves of *S. alabamensis* subsp. *alabamensis* for 1974 matched in size, color and conformation the largest leaves of wild plants from Chilton Co., Alabama, collected by Thomas Gibson and brought to Saginaw, Mi., for comparison.

Besides the size differences, each population differs in structural features which are not susceptible to precise measurement but which are nevertheless distinctive. Table 2 presents a comparison between the taxa for some of these and other features as do figures 5 and 6.

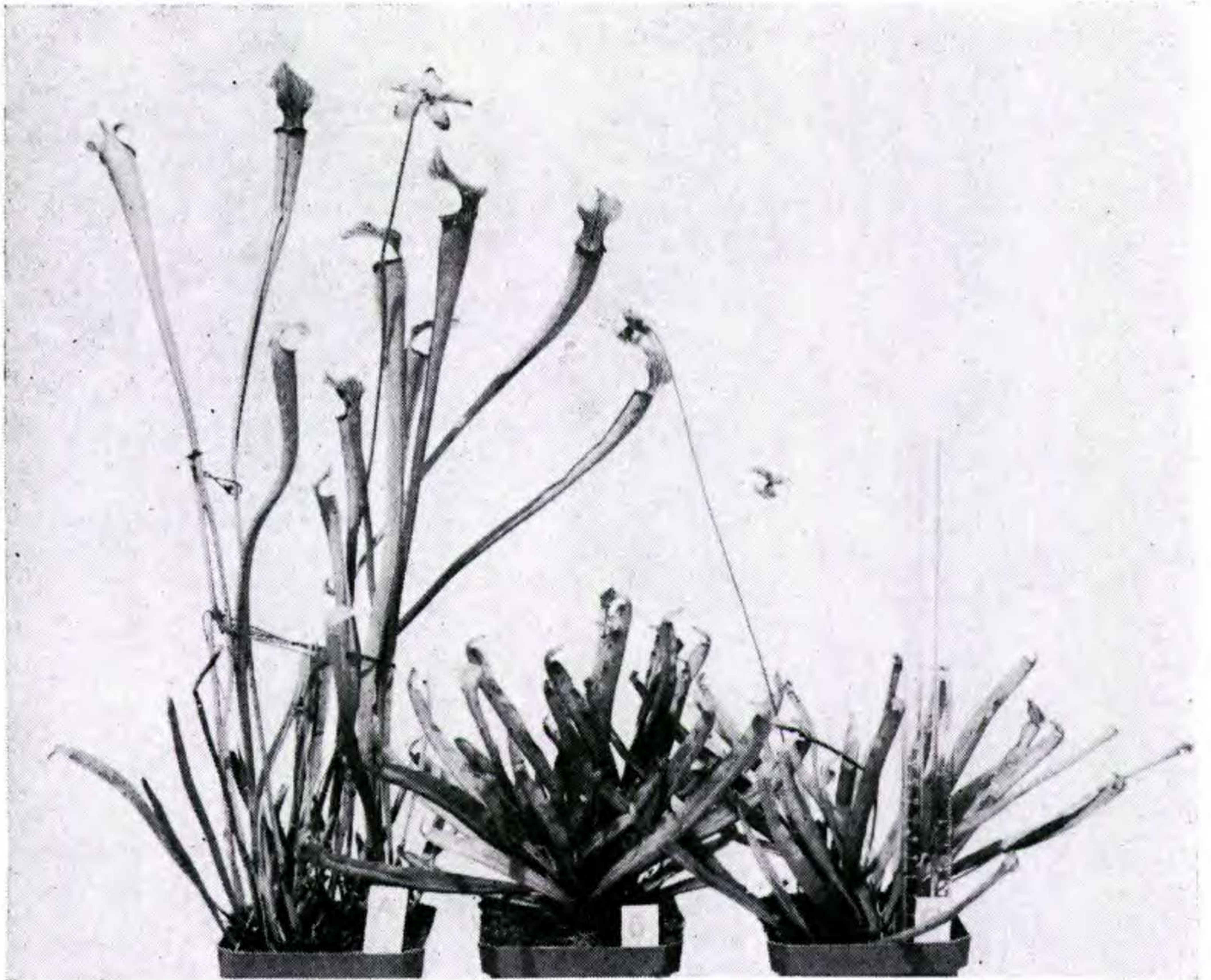


Fig. 5. A, *Sarracenia jonesii*, Transylvania Co., N. C. B, *S. rubra*, inner Coastal Plain plant from Lucknow, S. C., and C, *S. rubra*, from outer Coastal Plain near Georgetown, S. C. These 3 clones were grown 6 inches apart in an artificial bog garden outdoors at Saginaw, Michigan for 3 growing seasons. Plant B, when collected, had pitchers nearly as tall as those of *S. jonesii* and would have been considered an "intergrade" by some authors.

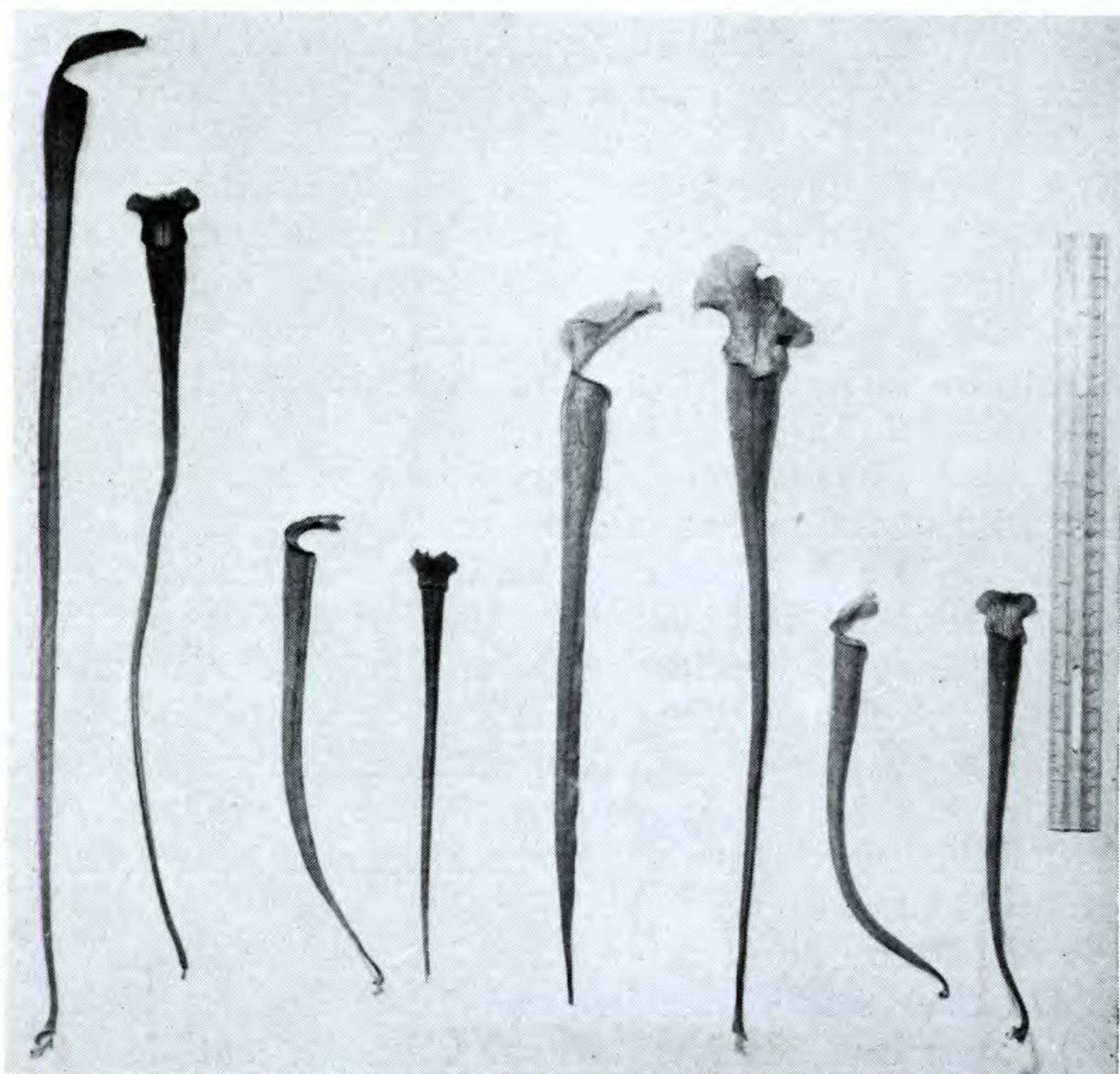


Fig. 6. Leaves of the 4 taxa comprising the *Sarracenia rubra* complex, selected because they approximate in size the mean for material grown under our comparative culture method. In pairs, left to right, *S. jonesii*, *S. rubra*, *S. alabamensis* subsp. *alabamensis*, and *S. alabamensis* subsp. *wherryi*.

It is particularly important to realize that the significant population groupings based on structural differences also represent populations geographically segregated from each other.

CHEMICAL INVESTIGATIONS

To see if comparative phytochemistry might show some significant trends within the *Sarracenia rubra* complex, we asked Dr. John Romeo, Chemical Plant Taxonomist, Oakland University, Rochester, Michigan, to examine our com-

parative culture plants. The work was carried out on all species of *Sarracenia* from our comparative cultures during June and July, 1975, at Oakland University, and at the University of Texas, Austin, Texas. Chemical analysis for amino acids and alkaloids, using chromatography and electrophoresis techniques, indicates only common protein amino acids present, with no significant differences between species. No alkaloids were detected by Romeo (personal communication, 1975).

Professors Romeo and Mabry also examined flavonoid compounds of all species of *Sarracenia* by paper chromatography. Study on these compounds is being continued by Romeo, Mabry, et al. The results of their chromatography allow no sweeping conclusions. The number of flavonoids present is too few, and the overlap of compounds between taxa too great to be of conclusive value in determination of speciation in the *S. rubra* complex. However, a pattern did emerge which we feel supports our conclusions drawn from structural and geographic data.

Plants of *Sarracenia rubra* from the inner Coastal Plain near Lucknow, South Carolina, and the outer Coastal Plain near Supply and Shallotte, North Carolina, and Georgetown, South Carolina, showed significant chemical differences from others of the complex in having two compounds present in large amounts which were not present in others of the complex, excepting in specimens of *S. jonesii* from Pickens Co., South Carolina, and Buncombe Co., North Carolina (but not all *S. jonesii* tested).

Four of five samples from Florida share a compound with three of four *Sarracenia jonesii* and one of the Carolina-Georgia Coastal Plain population. None of the other members of the *S. rubra* complex contains this compound, but it also occurs in *S. minor* and in two populations of *S. purpurea* tested.

Plants of the Flint River drainage in Taylor Co., Georgia, shared weak amounts of a compound in common with plants from Florida but differed from the Carolina Coastal Plain *Sarracenia rubra* in some compounds.

A compound present in most clones of *Sarracenia alabamensis* subsp. *alabamensis* occurs also in plants from Perdido, Alabama, but not elsewhere in the *S. rubra* complex. Plants of what we regard as belonging to the same basic population as those from Perdido, from near Fruitdale and Citronelle, Alabama, lack this compound. However, the Fruitdale-Citronelle area is one of particularly high incidence of hybridization among several pitcher plant species. McDaniel (1966) states "chemical introgression may occur in populations where extensive hybridization occurs." Considerable variation in trace amounts of four compounds in our material from this region suggests such introgression has indeed occurred.

The several pairs of populations which share flavonoid compounds between them which are not found elsewhere in the *Sarracenia rubra* complex suggest to us a relationship between them which agrees strongly with our geologic-geographic conclusions, and we will discuss it in that section of this paper.

TAXONOMIC TREATMENT

Field observation, structural differences, size differences, pitcher dimorphism in one population, and the isolation of clusters of subtle but distinctive traits in disjunct populations, clearly indicate that what has been called *Sarracenia rubra* consists of four or five discrete taxa depending upon where one draws the structural limits.

All of the populations appear superficially similar. It would be easy to call them all one species and to designate the individual populations as subspecies, but we do not feel that such a treatment would reflect a true evolutionary picture. There are other considerations. No two taxa are known to be truly sympatric and good evidence of intergradation between members of the different taxa does not exist. Plants such as those cited by Bell (1949) or McDaniel (1966) as intermediates between *Sarracenia rubra*

and *S. jonesii* can be shown to be ecological forms, or explained as complex hybrids (see discussion of *S. rubra*).

In our comparative cultures, in the greenhouse and out of doors, each taxon flowers at a slightly different time at a given locality; therefore, if they did grow together, interbreeding would not normally occur. Each population differs from the others in leaf size, color, texture, shape, hood size and shape, and in flower size and petal shape. One population differs substantially in producing dimorphic pitchers.

Hybrids formed between members of one population of the complex and a common other parent (*Sarracenia purpurea* subsp. *venosa*) differ in leaf size, proportion and texture from hybrids between members of other populations of the complex and the same common parent (fig. 7).

After careful consideration of our statistical data (Table 1) and of our field observations, and especially after our more than 20 years of observation of these plants growing under standardized conditions, we believe that the following taxonomic treatment best reflects the situation found in nature.

The following key relies primarily upon the types of leaves produced, and the characteristics of the fully matured, largest leaves of the growing season which have developed in bright sunlight. Because of the effects of ecological conditions pointed out in this paper, several specimens from a population will usually key better than a single specimen. Unless an herbarium specimen has been specially prepared and dried rapidly under heat, details of color, texture, and pubescence become obscured, rendering the specimen very difficult to use. We recommend, where possible, use of fresh leaves.

While we do not consider geographic location an ideal key character, the members of the *Sarracenia rubra* complex may be "keyed out" geographically, as each of the taxa is disjunct from the others of the complex. We have, therefore, included this information in the key.



Fig. 7. Leaf samples of hybrids between *Sarracenia purpurea* subsp. *venosa* and 3 members of the *S. rubra* complex: left to right, *S. jonesii* × *S. purpurea*, Transylvania Co., N. C.; two specimens, two clones, *S. rubra* × *S. purpurea*, Brunswick Co., N. C.; and *S. alabamensis* subsp. *wherryi* × *S. purpurea*, hand pollinated hybrid produced by us, both parents from Washington Co., Alabama. All leaves from flowering-sized plants in comparative culture, although we have seen and had leaves on the *S. jonesii* hybrid up to 3 times larger than the specimen pictured.

A KEY TO THE RED-FLOWERED, TRUMPET-LEAVED
SPECIES OF SARRACENIA

- A. Upper portion of pitcher-tube and hood strongly white-areolate, the areoles greatly exceeding in area the thicker, photosynthetic tissue between. Hood margins strongly undulate. Erect, gladiate laminar phyllodia usually present. *S. leucophylla*.
- AA. Upper portion of pitcher-tube and hood without areoles, or if areolate, obscurely and irregularly so, with pale yellowish-green or whitish-green areoles. Hood margins without undulation, or with a few irregular, broad undulations. Phyllodia, if present, few, obscure, recurved-decumbent. B.
- B. Pitcher tissue below orifice thick, almost waxy, the outer surface glabrous to puberulent (under magnification). Orifice rim tightly rolled, its juncture with the pitcher wing usually not indented, if indented, neither strongly so nor does indentation form a conspicuous, somewhat everted spout which extends forward over the pitcher wing. Orifice rim, major veins of both inner and outer pitcher tube, main and branch-veins of inner neck of hood strongly colored red-purple, the coloring of the hood veins extending to hood margins on both surfaces. Hood not reflexed or only slightly reflexed above neck. C.
- C. Pitchers 21-73 cm tall (average 45 cm), long petiolate, the solid petiolar portion up to $\frac{1}{3}$ the length of the leaf; abaxial portion of the petiole flattened in cross section, resembling an inverted T. Pitcher chamber diameter narrow, expanding sharply in upper $\frac{1}{4}$ of tube. Orifice diameter 1-4 cm wide. Neck of hood long, hood ascending, held high over the orifice, cordate, its margins weakly to moder-

ately reflexed, 2.4-6.5 cm long, 2.4-5.4 cm wide. Flower scapes about equalling pitcher height. Plant of the Blue Ridge Mountains of western Carolinas. *S. jonesii*.

CC. Pitchers 5.7-57 cm tall (average 21 cm), short petiolate, the solid petiolar portion less than $\frac{1}{4}$ the length of the pitcher; abaxial portion of the petiole rounded in cross section. Pitcher chamber diameter relatively narrow throughout, evenly and gradually tapered upwards, orifice 0.5-2.8 cm wide. Neck of hood short, hood usually carried close over orifice in a plane at nearly right angles to the long axis of the pitcher (less so in Florida population), its margins scarcely or not at all reflexed, 0.7-4.5 cm long, 0.7-3.9 cm wide, ovate. Flower scapes 1.5-2 times height of leaves. Plant of the Carolina-Georgia Coastal Plain and Fall Line Hills, with a disjunct area in western Florida. *S. rubra*.

BB. Pitcher tissue below orifice thin, densely fine-pubescent. Orifice rim loosely rolled, orifice at rim often slightly flared-everted, its juncture with the pitcher wing strongly indented and everted, forming a spout which extends slightly forward over the wing. Orifice conspicuously yellow-green. Upper pitcher green to golden-green, occasionally copper-red flushed. Major veins of upper pitcher-tube red-purple on inside of the tube only (although color may show through leaf tissue, especially in dried material). Veins of outside of hood of the same color as the tissue between veins. Veins of inner neck and hood, if colored, colored on main veins only, the colored portion not extending into puberulent distal portion of hood. D.

- D. Spring and late summer pitchers unlike in size, volume, and often shape; the spring leaves shorter, narrower, usually sigmoidly curved; flushed red-bronze when young. Summer pitchers not decidedly recurved, much exceeding spring leaves in height and volume, light clear green to golden-green, 18-71 cm tall (average 40 cm); orifice 1.7-6.7 cm in diameter. Area below pitcher rim with a few to many scattered obscure, light greenish-yellow to whitish areole-like mottlings on outer surface. Hoods very large, neck broad, hood 2.5-9 cm long, 2.2-8.8 cm wide, moderately to strongly reflexed, its margins with a few broad, irregular undulations. Mature hood tissue between veins conspicuously convex-puckered, yellow-green on outer surface. Veins of the hood uncolored above and in distal half below. Flower scapes 27-57 cm tall, exceeding the spring leaves and about equalling the summer ones. Plant of the Fall Line Hills of central Alabama north of the Black Belt soils.
 *S. alabamensis* subsp. *alabamensis*.
- DD. Spring and late summer pitchers essentially alike in size, volume and shape, dull green, flushed strawberry-bronze upwards, without areoles, 8-45 cm tall (average 18 cm); orifice 0.7-4.2 cm wide, tube often wider below orifice. Hood 0.8-4.5 cm long, 0.8-4 cm wide, overarching orifice to suberect, as wide or wider than long, veins of either surface varying from no red coloring to red-purple on major veins only, color extending to distal portion of hood only in some clones. Flower scapes 14-38.5 cm tall, equalling or slightly exceeding tallest leaves. Plant of southwestern Alabama and eastern Mississippi on both sides of the area of the confluence of the Tombigbee and Alabama Rivers.
 *S. alabamensis* subsp. *wherryi*.

1. *Sarracenia rubra* Walter, Fl. Carol. 152. 1788.²

Leaves semi-evergreen, dying back 1/3-2/3 only if severely frosted. Largest seasonal leaves of flowering plants relatively narrow throughout, gradually tapered from base to orifice, 5.7-57 cm tall, 0.5 to 2.8 cm wide; lateral wing relatively wide and prominent, often widest at or slightly below the middle, green becoming suffused with maroon tones in older, fully sunlit leaves, Florida forms often maturing to dark solid maroon colors. Leaf texture waxy, firm, rim of mature pitcher essentially horizontal (i.e. at right angles to main axis of pitcher); rolled rim not especially prominent, becoming dark maroon or dull green, the point of juncture of rim with lateral wing raised slightly or on the same level as the rest of the pitcher rim, or barely indented. Hoods as measured by us longer than broad, 0.7 to 4.5 cm long, 0.7 to 3.9 cm wide; ratio of length/width .98 to 4.3 in East Coast population, 0.8 to 1.5 in Florida population; hood suberect, carried close over the orifice; neck of hood not particularly contracted at base, the major veins and cross-veins of both outer and inner pitcher and hood surfaces becoming dark maroon-red with color spreading in Florida and west Georgia forms to mesophyll between vein reticulations, usually remaining green except on veins in Carolina material; veins of inside of hood colored maroon throughout entire distal, hirtellous portion (see fig. 6). Flower scapes erect, usually 2-3 times taller than tallest leaves, 17.0 to 66 cm tall in Atlantic coastal material, 26.5 to 48 cm tall in Florida population. Sepals 1.5 to 2.7 cm long, 2.0 to 2.6 cm wide, slightly narrowed or contracted beyond the middle in many individuals, maroon or greenish-maroon mottled on outer surface, the inner surface mostly green; lateral margins becoming strongly replicate over mid-line until they touch; calyx also recurving strongly away from the ovary after anthesis. Petals maroon, often on both surfaces, or with greenish suffusion on inner surface, panduriform, the basal cuneate

²For synonymy of *S. rubra* see Bell (1949).

portion relatively small, the distal lobe obovate, tending to be very strongly so; petals 2.5 to 4 cm long, the distal lobes 1.3-2.5 cm wide. Style disk 2 to 3.5 cm in diameter, 2-cleft, the margins of the cleft often overlapped. Mature capsules 0.5 to 1.5 cm in diameter, densely tuberculate.

Type locality: South Carolina, presumably on the Santee River.

Distribution: Very local, rapidly becoming rare in some districts, in bogs, swamps, and the Coastal Plain savannahs, or on springy hillsides near the Fall Line of Georgia, ranging from the Cape Fear River system in North Carolina locally southward to the Altamaha River system of the Atlantic Coastal Plain, southward ranging farther inland toward the inner Coastal Plain and Fall Line Sand Hills. Very local on the Flint River watershed system in western Georgia. A disjunct population more variable in leaf size and shape occurs in Walton, Santa Rosa and Okaloosa Counties in western Florida.

Representative Specimens: **Florida:** OKALOOSA CO., 3 mi W of Crestview, *E. T. Wherry* (PENN); Milligan, *J. M. MacFarlane* (PENN); 4 mi E of Crestview, *A. N. Leeds* (PH); swamp, Shoal River, *H. H. Hume* (DUKE); Adams Church near Crestview, *S. T. McDaniel* (FSU); margin of pond 1 mi E of Crestview, *R. K. Godfrey* (FSU); SANTA ROSA CO., 5.2 mi SE of Fla 87, vicinity of Yellow River N of Holley, *H. E. Ahles* (NCU); WALTON CO., ca 16 mi NE of Niceville, *J. Beckner, C. Chapman & R. R. Smith* (NCU); DeFuniak Springs, *A. H. Curtis* (US); margin of swamp, *A. H. Curtis* (NY). **Georgia:** BIBB CO., near Lakeside, *T. Darling, Jr.* (PENN); BULLOCK CO., Statesboro, *H. W. Trudell* (PH); COLUMBIA CO., 12 mi N of Augusta, *J. M. MacFarlane & W. Davis* (PENN); EMANUEL CO., bog in pine barrens near Graymont, *R. M. Harper* (NY); MACON CO., Toadover Creek, 8 mi SE of Reynolds, *J. H. Pyron & R. McVaugh* (PH); MONTGOMERY CO., swamp in sand hills west of Erick, *R. M. Harper* (US); SUMTER CO., sandy bog SE of Americus, *R. M. Harper* (US); sandy bogs, *R. M. Harper* (NY); TATTNALL CO., 1 mi S of Ochoopee, *R. M. Harper* (US). **North Carolina:** BRUNSWICK CO., Wilmington, *E. T. Wherry* (US); COLUMBUS CO., 4 mi S of Cerro Gordo, *C. R. Bell* (NCU); savannah near Brunswick, *A. E. Radford* (NCU); CUMBERLAND CO., vicinity of Fayetteville, *R. A. Clark* (DUKE); HARNETT CO., open bog, Overhills, *H. Laing* (NCU); HOKE CO., 4 mi SW of Montrose on Mountain Creek, *H. E. Ahles* (NCU); MONTGOMERY CO., 5½

mi SE of Candor, *A. E. Radford* (NCU); ONSLOW CO., Jacksonville, *H. J. Oosting* (DUKE); 2½ mi E of Onslow-Pender Co. line on NC 35, *H. E. Ahles* (NCU); RICHMOND CO., Hamlet, *W. W. Ashe* (NCU); SCOTLAND CO., 2.9 mi N of Silver Hill, *H. E. Ahles & R. S. Leisner* (NCU); 10 mi N of Laurinburg on Rt. 70, *C. R. Bell* (NCU); WAYNE CO., 5.8 mi E of Mt. Olive, *C. J. Burk* (NCU). **South Carolina:** CHESTERFIELD CO., between Cheraw and Sugar Loaf Mountain, *L. F. Ward* (US); CLARENDON CO., ½ mi S of Manning, *W. Stone* (PENN); COLLETON CO., *C. R. Bell* (NY); DARLINGTON CO., Hartsville, *J. B. Norton* (US); Seaboard R.R., W of Hartsville, *J. B. Norton* (NCU); GEORGETOWN CO., 5½ mi S of Georgetown, *R. K. Godfrey & Tyron* (NY); LANCASTER CO., near Kershaw, *H. D. House* (US); LEE CO., 2.7 mi N of Lucknow, *A. E. Radford* (NCU); LEXINGTON CO., 4 mi NW of Edmund, *A. E. Radford* (NCU); 5 mi S of Columbia, *Godfrey & Tyron* (US); thicket just N of Gaston, *E. T. Wherry* (PENN).

We restrict the epithet *rubra* to the plants from the Coastal Plain and Sand Hill regions of Georgia, North and South Carolina, and to the local disjunct population in Walton, Santa Rosa and Okaloosa Counties in western Florida. Plants of the Carolinas are the most uniform, tending to produce green, maroon-veined pitchers of small size and volume, a closely arching hood which is longer than broad, and without reflexed margins. The pitcher chamber tapers only slightly, the pitcher is nearly as wide below the middle as above it, and the point of juncture of rim and pitcher wing is often slightly raised. The scapes of the delicately small flowers usually exceed the leaves by 2-4 times.

Our concept of this species differs from that of MacFarlane, Bell, and McDaniel. MacFarlane did not recognize races or taxa within the *Sarracenia rubra* complex. Wherry, rightly as we believe, considered the Carolina mountain plants a distinct although allied species, *S. jonesii*. Unfortunately, the many shade ecads, introgressed hybrids of western Florida and Alabama, and plants of *S. alabamensis* from central Alabama confused him and he ascribed to *S. jonesii* a range in Alabama, Florida, and Mississippi which actually did not exist and which he later corrected (Wherry, 1972).

Most of the controversy over the *Sarracenia rubra* complex stems from the early misunderstanding of the nature and range of *S. jonesii*. Bell (1949), believing that the only reliable character which distinguished *S. jonesii* from *S. rubra* was the distinctive pitcher taper, and that this pitcher form occurred throughout the range of *S. rubra* reduced *S. jonesii* to a forma within *S. rubra*. He noted that many large Coastal Plain individuals lacked *S. jonesii*'s distinctive pitcher taper and he considered these large individuals as belonging to *S. rubra*.

McDaniel (1966) recognized that "*S. rubra*" consisted of more than one morphological form. He states:

Were almost any taxonomist unaware of the problem given selected specimens from Henderson Co., N. C., and selected specimens from the lower coastal plain of the same state, he would undoubtedly consider the two groups of specimens to represent two clearly distinct species. However, when all of the diversity of *S. rubra* throughout its range is considered, one must conclude that the form common in Henderson County and the form common on the lower coastal plain are extremes of the same species connected by intermediates both in North Carolina and in other states. . . . I believe that this species has basically four morphological expressions, each of which has certain geographic distributions. Intergradation between these forms is common and I do not feel it necessary or desirable to distinguish any or all of them as infraspecific taxa.

Several problems seem to have confused past taxonomists. First is the belief that the *Sarracenia jonesii* leaf form occurs anywhere except in the Carolina mountain counties. Contrary to McDaniel's statement that there are "selected specimens" from the mountains which are the "common" form, there is only one structural form manifested in the mountain counties, *S. jonesii*, and it occurs

only there. Plants from the Fall Line Sand Hills of Alabama represent *S. alabamensis* subsp. *alabamensis*, which produces small *S. rubra*-like spring leaves and large, somewhat *S. jonesii*-like summer leaves. Unusually large plants from the Gulf Coastal Plain represent either large ecads of *S. rubra*, extremes of *S. alabamensis* subsp. *wherryi*, or introgressed hybrid individuals (see discussion elsewhere in this paper).

There remains the problem of the citations of "intergrades" and of the relatively tall sand hill populations from the Carolinas, Georgia and Florida. We have seen no evidence that intergradation occurs at all. The Carolina *Sarracenia jonesii* is not known to make contact with any other members of the *S. rubra* complex. Indeed, it is separated from others of the complex by the Piedmont province which in the Carolinas is approximately 100 miles wide. Large-leaved plants of *S. rubra*, from the inner Coastal Plain and Fall Line Sand Hills, especially the herbarium material from Kershaw, Lee, Lancaster, Chesterfield, and Lexington Counties of North and South Carolina, and plants we collected from Taylor County, Georgia, approach the height of *S. jonesii*. Although they lack the distinctive sharply expanded upper pitcher chamber and the distinctive shape and carriage of the hood, they might easily be interpreted as intermediate forms. To determine if this large-leaf form was genetic or ecological, we collected specimens in the Fall Line hills of Taylor County, Georgia, in 1971 and from near Lucknow, Lee County, South Carolina, on the inner Coastal Plain in 1972. In both areas plants possessed unusually tall pitchers. We grew collected divisions of some of these clones in our comparative culture greenhouses and outside in our sand bog garden. Clones of each area were placed beside plants of *S. jonesii* from Henderson and Transylvania Counties, North Carolina and from Pickens County, South Carolina.

As pointed out by Mandosian (1966) the plants required time to adjust metabolic growth pools. The first leaves produced in cultivation, while smaller than those of *Sarra-*

cenia jonesii, remained larger than typical of outer Coastal Plain Carolina *S. rubra*. Those in the harsher outdoor garden situation became reduced in size most rapidly, but by the end of the third season both the comparative culture plants indoors, and the outdoor plants had reduced leaf size to that typical of outer Coastal Plain *S. rubra*, and all subsequent growth has remained so (see fig. 5). *Sarracenia jonesii*, in both indoor and garden culture has, meanwhile, retained its characteristic leaf shape and leaf size, even though in the outdoor bog garden both moisture and organic matter were below the amounts typical of *S. jonesii* habitat in the wild.

The so-called inner Coastal Plain intermediates between *Sarracenia rubra* and *S. jonesii* thus appear to be nothing more than ecads induced by the generally more shaded, peaty environment.

The disjunct colony of *Sarracenia rubra* in western Florida appears at first to be quite confusing. Within this area occur 1) plants which are typical, 2) plants typical in shape, but taller, and 3) plants much taller, some with rather erect, large, undulate hoods and some with tapered pitchers somewhat resembling those of *S. jonesii*. Particularly in dried specimens, the plants become difficult to place. Some of these unusual plants differ in color as well.

Anderson (1949) has pointed out that certain physical characteristics from one species may pass into another with which it is hybridizing independently of other characteristics, and may become established as a characteristic in the population of the introgressed species in its zone of contact. McDaniel (1966) in chromatographic experiments, suggests that chemical introgression may occur in *Sarracenia* populations where extensive hybridization occurs. He specifically found such evidence between *S. alata* and *S. leucophylla*. He feels (McDaniel, 1966, p. 20) that a degree of variability within certain species may be the result of such introgression. W. H. Camp (1949) published a note on *Sarracenia* in which he expressed the belief that there were no "pure" species in the Gulf Coast regions

at all, only massive hybrid populations. Camp overstated the situation, but hybrid populations abound in the Gulf Coastal Plain.

Along the Yellow River, in Santa Rosa County, Florida, is a mixed *Sarracenia* population in which the following are all fairly common: *S. rubra*, *S. leucophylla*, *S. flava*, *S. psittacina*, and *S. purpurea* subsp. *venosa*. Hybrids, backcrosses, and unusual genetic segregates occur between all species, except between *S. psittacina* and *S. purpurea*. They are most numerous between *S. leucophylla*, *S. rubra*, and *S. psittacina*, all red-flowered species with seasonal overlap in their flowering in this region. Variation in *S. rubra* here is unusually great. Genes from *S. purpurea*, *S. leucophylla*, and *S. psittacina* all apparently affect leaf carriage, color, and hood size and shape in *S. rubra*. Some clones from this region and a similar region south of Crestview, Florida, produce pitchers which at first appearance seem to show many of the characteristics of *S. jonesii*. The leaves are taller than those in ordinary *S. rubra*, narrower in their lower portion, and more sharply expanded upwards, with hoods arched higher over the orifice and more reflexed than in other *S. rubra* clones nearby. If one grows these plants and examines the nearly fully expanded but unopened pitchers, he will find small, faint, whitish areoles on the upper pitcher around the orifice and on the back of the hood, evidence of introgressive hybridization with *S. leucophylla*. *Sarracenia leucophylla* would also account for the unusual height of some of the *S. rubra* introgressants in the region.

Schnell (1974) commented on the large pitchers and the overall red-maroon coloring of many *Sarracenia rubra* plants of this population. One of the most noticeable traits of hybrids involving *S. rubra*, *S. purpurea*, *S. leucophylla*, and *S. psittacina* with other species is the presence in well lighted plants of an overall red-maroon flush to the leaf, the red coloring often being more developed than in either parent. F₁ hybrids involving these plants abound in this part of Florida (Bell, 1949, 1952; Bell and Case, 1956) and

most show this deep red coloring. This color, too, we feel has introgressed into the *S. rubra* population where it has enhanced the natural tendency to produce a red flush in the upper pitcher tube.

In bogs south and east of Crestview, Florida, grow large colonies of *Sarracenia rubra* in which the plants are shorter, and less suffused with red, much more in color and size like plants from Georgia and South Carolina. There is much less evidence of hybridization at these locations. Despite minor differences in color and size, and despite the great many unusual individuals, analysis of leaf size and structural features of this western Florida population shows that it most closely resembles the Atlantic Coastal Plain population and we place it in *S. rubra*. Our reconstruction of the group's geological history suggests that the Florida population has descended from the Chattahoochee or Flint River regions of Georgia, a conclusion also supported by our chromatological findings.

2. *Sarracenia jonesii* Wherry, Journ. Wash. Acad. Sci. 19: 385. 1929.

S. rubra forma *jonesii* (Wherry) Bell, Journ. Elisha Mitchell Sci. Society. 65: 137. 1949

S. rubra subsp. *jonesii* (Wherry) Wherry. Castanea. 37: 146. 1972

Largest seasonal leaves of flowering plants 21 to 73 cm tall, elongate at base, tapered, very narrow in lower portion of pitcher tube, becoming widely expanded mostly in the upper $\frac{1}{4}$ of the tube, often becoming so sharply expanded as to cause a cross-fold or notch-like fold in the adaxial face of the pitcher, with back of pitcher slightly bulged outward, 1 to 4.2 cm wide. Lateral wing of pitcher very narrow, widest below middle of leaf. Leaves firm and waxy textured, green, becoming veined with dark purple, or rarely with an overall deep maroon-black suffusion. Pitcher rim tightly rolled, dark maroon in sunlit leaves, indented somewhat at point where rim and lateral wing join. Hoods

2.4 to 6.5 cm long, 2.4 to 5.4 cm wide, ratio of length/width 0.91 to 1.67, hoods cordate, moderately reflexed, neck contracted, carried rather high over the clearly open orifice, veins of inside of hood colored maroon throughout, leaves semi-evergreen. Flower scapes few-many, erect, rarely exceeding the tallest pitchers of the season, 32.5 to 69.6 cm high. Sepals 2.5 to 3.5 cm long, 1.5 to 2.0 cm wide, broadly ovate, gradually tapered to a blunt tip, maroon or green-maroon mottled. Petals maroon 3.0 to 4.5 cm long, 2.0 to 2.8 cm wide, distal lobe often distinctly shovel-shaped.

Type Locality: Moist meadow 1.5 mi S of East Flat Rock Station, Henderson County, North Carolina, E. T. Wherry.

Type Specimen: U. S. National Herbarium No. 1,438,266. (Wherry).

Distribution: Native only to Buncombe, Henderson and Transylvania Counties, North Carolina, and in Pickens County, South Carolina.

Sarracenia jonesii thrives best in open boggy meadows. It was apparently frequent at one time in such habitats along Muddy Creek, in Henderson County, North Carolina. All known stations there appear to be extinct. Plants from the vicinity of the type locality are generally less heavily colored, and with somewhat shorter, broader pitchers than most of the *S. jonesii* from other stations, and resemble very closely in leaf many Mississippi plants of *S. alata*.

Sarracenia jonesii can also grow in brushy thickets along streams among alders and tangles of *Leucothoe* and other heaths. In such situations six or eight small colonies are known to survive.

Representative Specimens: **North Carolina:** BUNCOMBE CO., mountain bogs, Biltmore, Biltmore Herb. 3374a (NY); Biltmore Estate, F. E. Boyton (US); HENDERSON CO., 1½ mi S of Flat Rock, Wherry (US); East of Flat Rock, R. K. Godfrey (NY); East Flat Rock, D. Samson (NY); swamp near R.R. station, Etowah, E. T. Wherry (PENN); 1 mi S of East Flat Rock, Wherry & Pennell (PH); Hendersonville, H. H. Jackson (PH); near Edneyville, D. S. Correll (DUKE); **TRANSYLVANIA CO.,** boggy thicket, tributary of Little River, Case, Moore & Gibson (US). **South Carolina:** GREENVILLE CO.,

south slopes of Caesar's Head, *Loomis* (PH); south slopes of Caesar's Head, *Case, Moore & Gibson* (US); PICKENS CO. [GREENVILLE CO.?] stream feeding Mt. Lake, *C. R. Bell* (UNC).

Sarracenia jonesii is a rather tall-leaved plant distinguished from others of the *S. rubra* complex in its taller, relatively more slender pitchers having elongate petiole bases with most of the pitcher expansion in the upper quarter of the pitcher tube. Its distinctly cordate hoods are carried rather high over the orifice, and tend to be faintly undulate.

Flower size of vigorous plants of this species can be double that of others in the *Sarracenia rubra* complex, and the distal lobe of the petal tends to be more shovel-shaped than in others of the complex. Under uniform culture conditions the plants bloom about a week after all others of the complex.

Color of leaf and vein develops slowly in this taxon; young leaves seldom exhibit the overall red-maroon flush of developing, well lighted members of other taxa.

Several writers and correspondents have claimed that *Sarracenia jonesii* is merely an ecad of *S. rubra* and that the large, tapered pitchers result from special conditions of moisture, temperature, and light. Our experience indicates that this is a false assumption. We have grown plants of *S. jonesii* alongside *S. rubra* from inner and outer Coastal Plain stations, under identical conditions, for over 20 years. Regardless of the particular ecological conditions, it was the *S. rubra* taxa which varied most and at times became less like their wild counterparts. *Sarracenia jonesii* remained singularly constant and produced the large, sharply expanded pitchers throughout the growing season. Even when deprived of a generous water supply, *S. jonesii* pitchers, although becoming reduced in size, remain distinguishable from those of *S. rubra* in their taper, larger size, hood shape, length of petiolate base, and pitcher wing.

Schnell (1974, p. 8) states "How a plant may vary in different environments as compared to other members of the species which may vary differently or not at all in

transplanting, is still likely biologically significant." We concur, for while we agree that *Sarracenia jonesii* is very close to *S. rubra*, it has maintained its relative differences from that taxon. There can be no question but that these differences are genetic, not ecological.

We consider *Sarracenia jonesii* to be an extremely uniform, constant, relict species confined to the ancient Asheville Peneplain in the Blue Ridge Mountains. We agree with Wherry's assessment (1972) that he originally ascribed too large an area to this species (see discussion under *S. rubra*). The initial confusion led subsequent writers to suppose that the ranges of *S. rubra* and *S. jonesii* overlap, which they do not. The so-called intermediates and intergrades represent other species or unusual ecads of *S. rubra*. It is true that under conditions of deep shade, or if the rhizomes of *S. jonesii* are broken up by cattle trampling, the plants will produce numerous small leaves which overlap in size and shape those of *S. rubra*. Schnell (1974) points out that these are juvenile-type leaves. We agree. If grown under good culture, mature *S. jonesii* produces only tall, flared, distinctive pitchers. Many pitchers of *S. jonesii* cannot be distinguished from similarly sized pitchers of *S. alata* (Wood) Wood. No one seriously considers that *S. jonesii* belongs to that species!

Albino plants occur in at least one locality. This species is truly endangered; it would be a tragedy if its habitat were totally destroyed.

3. *Sarracenia alabamensis* Case & Case, *Rhodora* 76: 650. 1974.

subsp. *alabamensis*.

Leaves tending to be dimorphic or trimorphic. Spring pitchers smaller, 17.7 to 49.5 cm tall, sigmoidly curved, gradually but regularly tapered from narrow base to a rather broad orifice, 0.7 to 3. cm wide at orifice, clear green to yellow-green, often suffused in upper $\frac{1}{3}$ with strawberry-red when young, fading to yellow-green on

hoods. Veins uncolored on outer pitcher surface, strongly maroon-colored within. Lateral wing of pitcher wide, widest at or just below the middle. This highly expanded wing and recurved form of the spring pitcher may represent a transition to a phyllodium. Largest seasonal leaves (summer leaves) produced from early July onward in well lighted and well watered plants, much taller and larger than spring pitchers, 12.2 to 71.7 cm tall, 1.7 to 6.7 cm wide at orifice, densely but finely pubescent, pubescence deciduous in dried material, soft and thin textured, distinctly yellowish-green, often with faint pale yellow-greenish to whitish mottling in upper $\frac{1}{4}$ of pitcher, resembling obscure areolation — this condition rarely extending onto hood. Hoods of summer leaves large, undulate, with a puckered expansion of tissue between veins; 2.5 to 9 cm long, 2.2 to 8.8 cm wide, strongly and conspicuously reflexed, carried high, low, or irregularly over orifice, strongly apiculate. Rim of pitcher flared-out, loosely rolled, bright yellow-green, lacking maroon overtones, region of juncture of rim and lateral wing strongly indented — almost spout-like. Veins of hood colored only in basal half or not at all. Leaves evergreen only at bases, spring leaves fading and dying as summer leaves produced. Phyllodia produced intermittently, flat, decumbent, recurved, small, usually produced after spring and before summer leaves.

Flower scapes many, even on shaded plants, 27 to 57.2 cm tall, shorter than largest summer pitchers, although exceeding some spring ones, often several produced from one terminal bud. Sepals 2.0-3.0 cm long, 1.2 to 2.0 cm wide, ovate, gradually tapered to blunt end, maroon-green streaked, becoming rather strongly reflexed. Petals variably maroon, usually lighter than in *Sarracenia rubra* or *S. jonesii*, 2.6 to 4.2 cm long, 1.6 to 2.3 cm wide, margins of distal lobe often erose-denticulate. Mature capsules small, 0.6 to 1.0 cm wide.

Type Locality: Elmore Co., Alabama, along the railroad between Elmore and Speigner, Case & Case S-500 (US).

Distribution: In boggy places in the Fall Line Sand Hills (Harper 1922) of Elmore, Autauga, and Chilton Counties, Alabama.

Representative Specimens: **Alabama:** AUTAUGA CO., boggy bank near stream ca 7 mi E of Billingsly, *Case, Gibson and Smith* (US); CHILTON CO., Clanton, *C. L. Pollard & W. R. Maxon* (US); Jasmine, *R. M. Harper* (NY); sloping gravelly bog near Jasmine, *R. M. Harper* (US); gravelly bog near Adams, *F. & R. Case, et al.* (US); ELMORE CO., Elmore, *E. T. Wherry* (PENN); 1½ mi S of Speigner, *R. M. Harper* (PH); along the railroad between Elmore and Speigner, *F. & R. Case* (TYPE) S-500 (US).

Sarracenia alabamensis subsp. *alabamensis* is distinct from other members of the *S. rubra* complex in its production of small, usually recurved spring leaves and in the production of few to many large much expanded and voluminous summer and fall pitchers. These summer leaves are yellow-green, almost golden toned, faintly marbled with areole-like pale yellow-green to whitish markings, and with very large, expanded hoods. The spring leaves tend to remain more green-bronze red flushed. Both spring and summer pitchers tend to be short-lived and produced almost continuously during the season if moisture and light conditions are favorable. The plant is a dense clump former and a heavy bloomer.

Since publication of *Sarracenia alabamensis* we have received private communications, some of which suggest that the recurved spring pitchers described in the protologue are not normally produced in nature, but result from poor culture techniques. We have grown this species for 20 years and its behavior with respect to the recurved spring pitchers is consistent. It also produces the spring leaves in the wild (see fig. 8) (fide Thomas Gibson, personal observation, 1975). Plants transplanted to an experimental bog on the estate of C. F. Moore at Brevard, North Carolina, also produced the recurved leaves. *Sarracenia rubra* and *S. jonesii* growing next to this species either indoors or out in our experimental situations do not produce similarly curved spring leaves.



Fig. 8. *Sarracenia alabamensis* subsp. *alabamensis*, showing the large summer pitchers, and a few remaining recurved, smaller, spring leaves. Photograph from a color slide by Thomas Gibson, taken in Chilton Co., Alabama, September, 1975.

We may, in our original description of *Sarracenia alabamensis* subsp. *alabamensis* have emphasized too much the production of laminar phyllodia, for while some plants produce them, production is rare.

In our comparative cultures, *Sarracenia alabamensis* subsp. *alabamensis* blooms after subsp. *wherryi* and *S. rubra*, but before *S. jonesii*.

Since the original publication of this species, we have learned of a few somewhat more extensive colonies than we had previously believed still survived. We have visited one such large meadow colony of over 100 clumps. The geographic range is very limited, and like *Sarracenia jonesii*, the species is a relict in an area where suitable habitat, limited to begin with, and kept open by natural fires, has been rapidly destroyed by human activity. Even though there remain a few meadow colonies of a few hundred plants, most colonies, much smaller, exist only through the accident of habitat kept suitable through moderate pasturing by cattle. Should pasturing cease, the habitats would quickly return to brushy thickets in which, with modern fire protection, the pitcher plant colonies would be shaded out quickly. The species is endangered and deserves managed protection.

4. *Sarracenia alabamensis* subsp. *wherryi* subsp. nova

S. rubra Walter, Fl. Carol. 152. 1778 (in part).

S. jonesii sensu Wherry, Journ. Wash. Acad. Sci. 19: 385. 1929 (in part).

Tota planta subsp. *alabamensi* similis, sed folia vernalia magnitudine et forma foliis aestivalibus similia, 8-45 cm longa, ex rubro viridia, exareolata, ore 0.7-2.8 cm lata. A subsp. *alabamensi* operculis minoribus, suberectis vel orem impendentibus, tam latis quam longis vel latioribus, 0.8-4.5 cm longis, 0.8-4 cm latis, ex cupreo viridibus (non flavo-viridibus), venis viridibus vel coloratis, scapis brevioribus 13.7-45.5 cm altis, differt.

Differs from subsp. *alabamensis* in the following manner: Rhizome: sparsely branching, clump forming tendency only moderate. Pitchers not noticeably dimorphic, petiole, recurved-ascending; tubular portion more or less erect. Pitchers 8 to 48 cm tall, 0.7 to 2.8 cm wide at orifice, often stout, frequently very gradually tapered from the base to orifice, not flared, but with the pitcher taper widest below the orifice. Pitchers densely fine pubescent, green to bronze-green, upper portion and hood flushed salmon-pink, external veins mostly without dark maroon coloring, major veins dark maroon-purple within (dark color may show through giving a false impression of coloring in external veins, especially in dried specimens). Hoods wider than long, variable, convex and weakly reflexed in most plants from the southwestern corner of the range, more erect, reflexed and with undulate margins in the northern and northeast corner of its range; veins of the underside of the hood heavily colored maroon-red in the neck and proximal portion, uncolored to colored only on a few of the main veins extending into the hirtellous distal region, veins of hood exterior scarcely if at all colored. Pitcher rim not flared out, moderately outrolled, yellow-green, moderately indented at juncture of orifice rim and lateral wing.

Flowers very early, scapes short, 13.7 to 45.5 cm tall, produced before development of pitchers, and barely equaling or exceeding pitchers; relatively large, 3.9-6.1 cm wide. Petals maroon-red often yellow streaked or orangish, but dark red-maroon in northeast portion of its range, distal lobe strongly obovate. Sepals broad, not strongly reflexed, 2.3 to 3.0 cm long, 1.5 to 2.0 cm wide, bluntly rounded. Style umbrella 3.2 to 4.2 cm wide, the divided tips of the lobes rounded at their apex.

TYPE: Common along a swampy trough in the pine woods about $\frac{1}{2}$ mile east of Chatom, Washington Co., Alabama, growing with *S. leucophylla* Raf. *F. & R. Case* S-573 (US), collected July, 1972, but prepared from cultivated material in September, 1974.

Distribution: Northern Baldwin Co., western Escambia Co., and Washington Co., Alabama, and Wayne Co., Mississippi.

Representative Specimens: **Alabama:** Baldwin Co., 12 mi E of Bay Minette, *S. T. McDaniel* (FSU); Bay Minette, *J. M. MacFarlane & C. Goesty* (PENN); 10 mi N of Bay Minette, *LeClair* (UNC); WASHINGTON CO., damp pine barren between Chatom and Deer Park, *R. M. Harper* (NY); 3 mi NW of Fruitdale, *S. T. McDaniel* (FSU); 4.5 mi W of Chatom, *S. T. McDaniel* (FSU); 4 mi N of Deer Park, *S. T. McDaniel* (FSU); 10 mi N of Citronelle, *S. T. McDaniel* (FSU); swampy trough in pine woods, ½ mi E of Chatom, *F. & R. Case* S-573 (Type). **Mississippi:** WAYNE CO., Waynesboro, *C. L. Pollard* (NY), (US).

Sarracenia alabamensis subsp. *wherryi* occurs in the pineland bogs of Wayne Co., Mississippi, Washington County, Alabama and east of the Tombigbee and Alabama River systems, much more sparingly in northern Baldwin and western Escambia Counties, Alabama.

This subspecies is locally abundant in ditches and pineland bogs in the western parts of its range, yet it seems not to have penetrated very far into Mississippi, nor to have reached the rich *Sarracenia* bogs southwest of Mobile, Alabama.

We dedicate this subspecies to Dr. Edgar T. Wherry, whose insights into Sarraceniaceae are particularly clear, and who has been so generous with his time, information and assistance to professional and amateur botanists alike.

Sarracenia alabamensis subsp. *wherryi* has pitchers much like the spring leaves of subsp. *alabamensis* in color, pubescence, texture and markings. The pitchers, however, lack the sigmoid curve so common in spring leaves of subsp. *alabamensis*, and tend to be recurved only in the petiolate base. Summer pitchers are of the same sort as the spring ones and only slightly larger; they lack the strong yellow undertones and obscure whitish areolations. Flowers in this taxon are larger, on shorter stems, with very obovate petals, and fewer are produced per plant.

Whereas the majority of plants of this population are quite distinct, some plants resemble plants of the Florida

population of *Sarracenia rubra* in general size and shape. Although there is no herbarium evidence of contact between these two populations, and we have found no evidence in our field work, the distance between the populations is not great and some gene flow between them could have occurred which might account for some of the similarities. However, the eastern segment of the population of subsp. *wherryi* varies less; many of the plants which most closely approach *S. rubra* here grow in the western edge of the area, in southern Washington Co., Alabama, where hybridization with *S. alata* and others is rampant. We are inclined, therefore, to believe these confusing plants have resulted from introgressive hybridization with *S. alata*, *S. psittacina* and *S. leucophylla* rather than from intergradation with *S. rubra*.

Since leaf substance, pubescence, general shape and volume, color and hood features of subsp. *wherryi* are most similar to the same features in comparable leaves of *Sarracenia alabamensis*; since the populations occur partly on the same river system, separated only by 100 miles of unsuitable Black Belt soils; and because plants from this population from near Perdido, Alabama, when chromatographed shared in common with most plants of subsp. *alabamensis* a flavonoid compound not found in others of the *S. rubra* complex, we place this plant as a subspecies of *S. alabamensis* while we acknowledge that its origin could be more complex.

GEOLOGICAL HISTORY AND SPECULATION

In his "Distribution of North American pitcher plants", Wherry (1935) theorizes that our modern sarracenias originated on the old pre-Cretaceous [Schooley or Cumberland (Fenneman, 1938)] peneplain of eastern North America somewhere between the limits of glaciation and the present day Fall Line. At that time, our present day Coastal Plain did not exist, but authorities agree that conditions of moisture and climate on the old peneplain

were fairly similar to modern-day conditions on the Coastal Plain (Wherry, 1935; Braun, 1950). Tertiary uplifts later created the present Appalachian-Cumberland regions, destroying the old boggy peneplain conditions, while the resulting erosion deposits and crustal movements caused development of the Coastal Plain lowlands. As most suitable *Sarracenia* habitat in the Tertiary uplands was slowly destroyed, the plants presumably spread down onto the developing Coastal Plain which is their center of occurrence today.

Wherry's generalized account agrees well with the theories and evidence presented by other plant-geographers (Cain, 1944). In the study of relict species on the Blue Ridge or Cumberland Plateau of plants very local there and more abundant on the Coastal Plain, *Sarracenia* is often cited.

With so much attention having been given to the geological history of this region, it is interesting that no one has previously examined this history in relation to the *Sarracenia rubra* complex. Each of the major disjunct populations of the *S. rubra* complex centers around the swamps of a major river system which today has or in the past has had its headwaters in or very near to Henderson, Transylvania or Buncombe Counties, North Carolina, and Pickens and Greenville Counties, South Carolina, or can be shown to have had headwaters connections in the past into the French Broad-Tennessee River region just west of the Great Smoky Mountains. In that region of the western Carolinas, an ancient strath or peneplain (Asheville Peneplain, Fenneman, 1938) survived largely intact the geological upheavals which destroyed most of the pre-Cretaceous peneplain elsewhere in the region (Fenneman, 1938). Especially at its southern end, the incipient peneplain lacked sharp drainage (Fenneman, 1938). That it remained suitable for pitcher plants is evidenced by the presence there today of *S. jonesii* and *S. purpurea*. Three major rivers pertinent to this study arise in this area, the Chattooga, Saluda, and the French Broad. Headwaters of

the Catawba, Peedee and Cape Fear Rivers arise just over the divides to the east and northeast.

One may speculate as follows upon the past events. The common ancestor of the modern *Sarracenia rubra* complex survived the Tertiary Uplifts in the ancient Asheville Strath. In the early history of this region, the Chattooga River was continuous with the Chattahoochee River (via Deep Creek, Fenneman, 1938). There was, therefore, a past direct corridor from the ancient mountain strath bogs to the Fall Line hills habitat of western Georgia, over which pitcher plants or their propagules might migrate. Along this route, and across divides of only a few miles lie the headwaters of the Flint and Ocmulgee Rivers where *S. rubra* grows today. From these sand hill regions migration downstream and across rather narrow divides could have taken place from the lower Chattahoochee to the southwestward flowing rivers which drain the area just east of Pensacola, Florida, where the disjunct colonies of *S. rubra* occur on the Coastal Plain today.

At a later time, the upper Chattahoochee (Chattooga) was captured by the headward growing Savannah River (Fenneman, 1938, p. 136-137) and the westward shift of the Blue Ridge divides as the east coast rivers with steeper gradients extended their headwaters (Fenneman, 1938, Dietrich, 1971). A series of migration corridors, direct via the Chattooga-Savannah Rivers, and somewhat less direct, through the westward shift of the Blue Ridge divides (Fenneman, 1938), opened up to the Atlantic Coastal Plain swamps. That it is possible for pitcher plants to cross this Blue Ridge divide along these streams is attested to by the presence of "cataract colonies" (Wherry's term) of *Sarracenia jonesii* along streams draining to the Atlantic today at an elevation well below the elevation at which the bulk of the *S. jonesii* population grows in its main range west of this divide in the French Broad (Mississippi) drainage.

In this manner, apparently, the ancestor of the present eastern *Sarracenia rubra* migrated from this mountain

area into the drainages from eastern Georgia to the Cape Fear River. Limited lateral spreading through the outer Coastal Plain swamps probably occurred in this area.

West of the Coosa in Alabama grow *Sarracenia alabamensis* subsp. *alabamensis* and subspecies *wherryi*. Evidence of the early history of these taxa is less direct. The Coosa drains from the Great Valley region (Fenneman, 1938) between the Tennessee River and the Great Smoky Mountains, near the Tennessee-Georgia state line, but has tributaries from the east which reach nearly to the Chattahoochee. The French Broad River, older than the Appalachians (Fenneman, 1938), crosses them and flows through the Great Valley to the Tennessee. Although postulated by some authorities, a direct connection from the Tennessee River to the Coosa has not been demonstrated.

It is possible that the ancestor of *Sarracenia alabamensis* originated in the area occupied by *S. jonesii* today, and that it reached the Coosa headwaters either via the French Broad drainage along which today the bulk of the *S. jonesii* population occurs, or via the Chattahoochee corridor to the lower Coosa tributaries.

Since *Sarracenia alabamensis* differs more from *S. jonesii* and *S. rubra* than the latter two differ between themselves, it seems most likely that before the Tertiary uplifting, a common ancestor to the *S. rubra* complex occurred not only in the Asheville Peneplain, but in the regions farther west of the Great Valley and Cumberland Plateau. This ancestral stock became separated by the events which formed the Appalachian Mountains and in the west became obliterated. Before the western form became extinct in the Cumberland Plateau region, some of its members reached the headwaters of the Coosa and descendents found their way to the Fall Line Sand Hills of Alabama where they survive in a limited area today.

At a later date descendents of this population crossed the Black Belt soil barrier and evolved into subsp. *wherryi* near the Alabama and Tombigbee Rivers north of Mobile Bay.

In the course of the long history involved in these migrations, the localized, isolated populations became changed from one another, perhaps through genetic drift, mutation, and hybridization with other species.

That this has been the method of development of the *Sarracenia rubra* complex, rather than through the extinction of parts of a once more or less continuous Coastal Plain or Fall Line population, is evidenced in several ways: those populations which occur on the same or a historically related river system resemble each other structurally more than do those members of the complex on river systems with a different history; the absence of *S. rubra* from many Coastal Plain swamps which are, however, occupied by other species of sarracenias (i.e., *S. flava*, *S. leucophylla*, *S. psittacina*), suggests to us not that the former Coastal Plain range of *S. rubra* has been reduced, but rather that members of the *S. rubra* complex have descended from an ancient stock which during the Tertiary times became broken into small, isolated populations which have become so adapted to their particular habitats that they lack the genetic aggressiveness to colonize extensively.

All members of the *Sarracenia rubra* complex are extremely winter hardy. We grow all species of *Sarracenia* outdoors at Saginaw, Michigan, where winter temperatures (often without snow cover) commonly fall to minus 18°C, and may reach to minus 30°C. Such a degree of hardiness suggests to us a more upland or interior developmental history rather than an origin on the rather mild Coastal Plain.

Of particular interest is a finding from the chromatographic study of this complex. Several "pairs" of disjunct populations share flavonoid compounds which were not generally present in other populations of the complex (see Table 3).

In each instance, the population on the geologically younger Coastal Plain occupies swamps in the vicinity of a major river system which drains from an older, Fall Line or Blue Ridge region occupied by the other population with

TABLE 3

Inland, Geologically older Fall Line or Blue Ridge Region		Outer Coastal Plain, Geologically Younger Region
<i>S. jonesii</i> , Western Carolinas	←→	<i>S. rubra</i> , Western Florida
<i>S. rubra</i> , Taylor Co., Georgia	←→	<i>S. rubra</i> , Western Florida
<i>S. jonesii</i> , Pickens & Buncombe Counties, S. & N. Carolina (but not all <i>S. jonesii</i> tested)	←→	<i>S. rubra</i> , Carolina Coastal Plain.
<i>S. alabamensis</i> subsp. <i>alabamensis</i> , Chilton, Autauga, Elmore Cos., Alabama	←→	<i>S. alabamensis</i> subsp. <i>wherryi</i> , vicinity of Perdido, Baldwin Co., Alabama

Table 3. Regions of occurrence of *Sarracenia rubra* complex taxa which share a flavonoid compound which is not generally present in the other populations of the complex.

which it shares a compound. The presence of a compound not found elsewhere in the *Sarracenia rubra* complex in two disjunct populations on the same river drainage system suggests to us a relationship between them which supports our construction of the group's history. It does not seem likely to us that coincidence could account for all of the compound sharing pairs of disjunct populations to occur on just the "right" river systems to fit our historical reconstruction.

When all the evidence is considered, we believe that the species which constitute the *Sarracenia rubra* complex derive from a common pre-Cretaceous ancestral stock which became discontinuous due to Tertiary geological events. Two surviving segments of the original ancestral population, one east and one west of the Appalachians, managed to migrate along definite routes to Fall Line or Coastal Plain areas. Another descendant survived in the ancestral Blue Ridge home area as well. During the course of these events, the various populations have diverged to form three closely related species.

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